DIETS OF JUVENILE FLATFISHES NEAR KODIAK ISLAND, ALASKA

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THESIS

Presented to the Faculty

of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

FISHERIES OCEANOGRAPHY

MASTER OF SCIENCE

By

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Fairbanks, Alaska

December 2001

ABSTRACT

Flathead sole, Pacific halibut, rock sole, and yellowfin sole were found co-existing near Kodiak Island as juveniles (<200 mm) during late summer. Dietary differences were attributed to fish species, size, and depth–sediment characteristics of their habitat. Two to three size classes were assigned within each species. Across all habitats, significant differences in dietary composition, stomach fullness, and diet diversity were found between size classes of different flatfish species. Within a single depth–sediment habitat, flatfishes of different species and size classes ate similar prey. Seven of nine species size classes had similar prey composition across multiple habitats. Significant differences in dietary composition across habitats were detected only for small Pacific halibut and small rock sole. The juvenile flatfishes near Kodiak were opportunistic feeders, and appeared to select habitat based on parameters other than the presence of specific prey taxa.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ACKNOWLEDGMENTS

Foremost, I thank my dear friend, mentor, supervisor, and committee chair, Brenda Norcross, for the guidance and encouragement she has given throughout my professional career. I thank Howard Feder, Thomas Shirley, Ron Smith, and Waldo Wakefield, the remaining members of my committee, for their constructive criticism on drafts of this thesis. The direction of my career in oceanic science has been influenced greatly by Howard, Ron, and Brenda. As an undergraduate, my most interesting scientific courses were the ones Howard taught in marine invertebrate zoology and Ron taught in biology of marine organisms. From the first days of my job with Brenda, she shared her enthusiasm for working on the ocean, and the joy of fieldwork has never left me. My family has helped me both before and during my tenure as a graduate student by encouraging me continuously, pushing me occasionally, and helping me financially. In particular, I thank my mother, Wendy Beverstock, for seeing no limit to my potential. My family and friends helped keep me on the path I had chosen, and I greatly appreciate their support.

Brenda Norcross, Franz Mueter, Bruce Short, Gary Edwards and the crew of the *F/V Big Valley* helped with field collections, and Ken Coyle assisted with invertebrate taxonomy. Funding for fish collections and laboratory analyses was provided by Saltonstall-Kennedy through NOAA grant #NA-16FD0216-01, and by the Coastal Marine Institute of the University of Alaska Fairbanks through grant #14-35-0001-30661. Additional support for travel to scientific meetings was provided by the Graduate Program of Marine Sciences and Limnology and by the School of Fisheries and Ocean Sciences.

INTRODUCTION

Juveniles of several species of flatfish concurrently occupy nursery areas in nearshore Alaskan waters during summer. The most abundant pleuronectid species of south-central Alaska include flathead sole, *Hippoglossoides elassodon* Jordan and Gilbert, Pacific halibut, *Hippoglossus stenolepis* Schmidt, rock sole, *Pleuronectes bilineatus (*Ayres) and *Lepidopsetta polyxystra* Orr and Matarese[1], and yellowfin sole, *Pleuronectes asper* Pallas (Norcross *et al.*, 1995; Abookire and Norcross, 1998). These flatfishes are of interest due to their high economic value in commercial and sport fisheries. Increased knowledge of the early life history of these fishes would benefit species management. The 1996 Sustainable Fisheries Act (Public Law 104-297) emphasized the importance of defining and protecting essential fish habitat, and van der Veer and Nash (2001) recommended assessment of the qualitative and quantitative use of habitats by flatfishes. The spatial and temporal overlap of several flatfishes as juveniles presents a scientific puzzle as to how multiple similar species can live sympatrically. The degree to which juvenile flatfishes share spatial and trophic resources and the relative importance environmental and biological factors on patterns of abundance are unknown.

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[1] The present research did not distinguish between the two species of rock sole that are sympatric in the study region (Orr and Matarese, 2000). The two species are *Pleuronectes bilineatus (Ayres)* and *Lepidopsetta polyxystra* Orr and Matarese.

Patterns of age-0 and age-1 flatfish distribution and abundance are attributed to depth and substrate near Kodiak Island (Norcross *et al.*, 1993, 1994, 1995, 1997; Chilton, 1997), near the Alaska Peninsula (Norcross *et al.*, 1999), and in lower Cook Inlet (Abookire and Norcross, 1998) (Figure 1). Juveniles of the four species of flatfishes examined near Kodiak by this study are distributed across a wide range of depths and sediment grain sizes. Habitat type is hereafter described in terms of depth and sediment, i.e., the term "deep gravel" indicates a depth range 40–90 m and sediment of gravel-sized particles. Flathead sole are caught in relatively high abundance at deep sites with a variety of sediments. Halibut are caught in high abundances at shallow gravel, and at shallow and deep sandy areas. Rock sole is relatively abundant at shallow and deep areas with gravel or sand substrate. Yellowfin sole are most abundant within shallow areas of gravel or mud substrates. Studies of flatfish distribution and abundance in south-central Alaska defined ages of juvenile flatfishes based on size of fish and used depth and/or sediment grain size to describe habitat. However, apparent preferences of these fishes for depth and sediment can vary with geographic area (Norcross *et al.,* 1999). Abundances also can vary considerably within a defined habitat, and neither presence nor abundance of one of these species is guaranteed by presence of its preferred habitat (Norcross *et al.*, 1999). The sympatric occurrence of the four closely related juvenile flatfishes and

the wide variation in levels of abundance within a habitat (Norcross *et al.*, 1997, 1999) suggest a need to evaluate trophic resource partitioning.

The description of diet relative to the size of fish and habitat (e.g., Toole, 1980; Lang and Livingston, 1996; Orr and Bowering, 1997) may be particularly relevant for flatfishes because of the extreme changes in morphology and ecology this group of fishes exhibits. Flatfishes are unique among fishes because, along with the ontogenetic increases in mouth size, overall body length, and swimming speed, flatfishes undergo the morphological and ecological transition from bilaterally symmetrical pelagic larvae to asymmetrical and demersal adults. The gradual physical metamorphosis of a flatfish, wherein one eye migrates over the top of the head so that both eyes are on one side of the fish, is accompanied by extensive changes in behavior and habitat of newly settled to late juvenile fish. Mouth structure (Tsuruta and Omori, 1976; Allen, 1982; Hacunda, 1981; Piet *et al.*, 1998) and body size influence which prey a juvenile flatfish can successfully pursue, capture, swallow, and digest. Mouth gape is the most important morphological constraint affecting food choice of juvenile flatfishes (Hacunda, 1981; Piet *et al.*, 1998). Other features of mouth morphology affecting diet include dentition and orientation of jaws during foraging (Allen, 1982). Competition between juvenile flatfishes is greatest when their mouths are small (Piet *et al.*, 1998), limiting the prey taxa they are able to engulf. Relative differences in mouth size to fish length are apparent among the four species

examined in this study. Mouths of flathead sole and Pacific halibut are relatively large, while rock sole and yellowfin sole have small mouths (Hart, 1980).

The temporal and geographic overlap and similar morphologies of flatfishes suggest a large potential for interspecific and intraspecific competition for space and prey. Density-dependent feedbacks may be particularly strong in flatfishes because of the reduced dimensionality of feeding environment that accompanies transition from a pelagic larval to a benthic juvenile stage (Cowan, 1997). Density-dependent regulation of abundance via competition for prey is most likely to occur in flatfishes during the late-larval or juvenile stage. Interspecific competition may be a major factor structuring the juvenile flatfish assemblage in the North Sea (Cowan, 1997). Competition for prey may affect habitat quality for juvenile fishes congregating in nurseries, particularly in regions of limited food availability (Gibson, 1994). Suboptimal habitat leads to reduced growth (Sogard, 1994), prolonging vulnerable life stages and resulting in a greater probability of mortality by predation. Slight differences in geographic distribution of potentially competitive fishes may limit the actual competition for a prey taxon eaten by multiple species. Localized partitioning of food resources is found among co-occurring species of adult (e.g., Kravitz *et al.*, 1977; Stickney *et al.*, 1974; Pearcy and Hancock, 1978; Livingston, 1987; Orr and Bowering, 1997) and juvenile flatfishes (e.g., Edwards and Steele, 1968; Gibson, 1973; Hogue and Carey, 1982; Sturdevant, 1987). In the latter studies, potentially competitive

interactions between predator groups were limited by spatial or temporal variations in feeding location or by increases in diversity of diet.

The present research hypothesizes that dietary composition of four juvenile pleuronectid flatfishes is related to fish size, physical habitat parameters, and fish abundance. Objectives are to (1) describe the diets of four abundant and co-occurring juvenile flatfishes and (2) provide a concurrent assessment of the spatial distribution of flatfishes and their prey. The first objective describes diets over a size range of fishes that previously has not been examined in detail. The second objective contributes to better understanding of the interactive effects of diet and habitat selection in nearshore nurseries.

METHODS

SAMPLE COLLECTION AND PROCESSING

Samples of fishes and sediment were collected at 103 sites during a study of juvenile flatfish distribution near Kodiak Island, Alaska (Norcross *et al.*, 1993, 1995), and flatfish diet was analyzed at 82 of these sites (Figure 2). From 11 through 25 August 1991, samples were collected from northeastern Kodiak toward the south of the island. More than half of the sample sites were at northeastern Kodiak, in Chiniak Bay. Tow sites encompassed a 1–90 m depth range, and a variety of sediment grain sizes from coarse gravel to fine mud. Sediment was collected at one point near the tow track using a 0.06 m^3 Ponar

sediment grab. Fishes were caught using a 3.67 m plumb staff beam trawl with 7 mm stretch mesh and a codend liner of 4 mm bar mesh (Gunderson and Ellis, 1986). All fishes were identified and total length (TL) measured. Flatfishes retained for diet analysis were surrounded with flaked ice immediately after capture, frozen within six hours, and returned whole to the laboratory.

Collection of fishes was limited to daylight and flood tide to reduce diel and tidal variations in fish diet. Juvenile pleuronectids are generally visual feeders (e.g., Holmes and Gibson, 1986; Gibb, 1995), although chemoreceptors and mechanoreceptors may also aid in prey detection (Batty and Hoyt, 1995). Feeding behavior of flatfishes can be strongly related to diel activity (Gwyther and Grove, 1981; Langton, 1983; Lang *et al.*, 2000) and tidal cycle (Marchand and Masson, 1989). Cyclic behavioral patterns are also observed in taxa typically eaten by flatfishes, such as decapod crustaceans, amphipods, and harpacticoid copepods (e.g., Pearcy *et al.*, 1977; McCall, 1992; Zouhiri and Dauvin, 1996; Takahashi *et al.*, 1999).

Abundances of juveniles of all 11 species of flatfish captured were initially calculated using a catch-per-unit-effort of number of fish per 10 min. tow (Norcross *et al.*, 1993). A total of 5,026 individuals <200 mm TL were captured of the four abundant species, including 574 flathead sole, 284 Pacific halibut, 2,724 rock sole and 1,444 yellowfin sole. Based on literature (e.g., Hart, 1980) and length frequency analyses (Norcross *et al.*, 1993, 1994, 1995), 200 mm TL is equivalent to

age-≥2 for each of these species. Some individuals of age-2 flathead sole and rock sole may have reached sexual maturity, but Pacific halibut and yellowfin sole are not adult until the respective ages of ≥5 yr (St-Pierre, 1984) and 4 yr (Salveson and Alton, 1976). Thus the samples examined in the present research may include a few adult flathead sole and rock sole in addition to juvenile fish of each species.

Each species was subsampled by including fish only from sites where stomach contents were examined of each captured individual of that species. The number of fish processed for stomach contents was 1542, including 349 flathead sole, 201 Pacific halibut, 673 rock sole and 319 yellowfin sole. No evidence of regurgitation was found during cursory observation of the mouth and gill rakers. After thawing a fish, its length was measured (TL). The stomach was excised at the esophagus and pyloric caecum, and proportional stomach fullness recorded (i.e., 0, 5, 25, 50, 75, 100%). No stomach was distended beyond 100% full. Prey taxa were identified to the most specific taxonomic level practical within time limitations, counted, preserved in 50% isopropyl alcohol for up to two weeks, and weighed (0.1 mg). For each prey taxon, whole individuals and heads were counted; if no heads were present, all fragments assigned to a taxon were combined into a count of one individual, regardless of the number of fragments. Storage of prey in alcohol may have affected biomass by removal of lipids. However, loss of prey weight was not considered in this study.

Sediment from each tow site was subsampled for grain size analysis and identification of benthic fauna. Grain size was evaluated using the Wentworth scale (Sheppard, 1973), where gravel (pebble and granule fractions) is 64–2 mm, sand is 2–0.063 mm, and mud (silt and clay fractions) is <0.062 mm. Weight percents of gravel, sand, and mud were obtained using a wet sieving technique (Folk, 1980). If the sediment grain size was ≥30% gravel, the sediment was categorized as gravel; if the gravel proportion was <30%, the sediment was categorized as sand or mud, whichever was the largest portion (after Norcross *et al.*, 1995, 1997). In an effort to directly assess prey availability, sediment samples were sieved over a 1 mm screen and fauna were sorted into broad taxonomic groups, e.g., amphipods, cumaceans.

Collections were stratified post hoc into six habitat categories defined to facilitate cross-species comparisons. Habitat categories were based on depth and sediment grain size, and were similar to established patterns of flatfish species abundance (Norcross *et al.*, 1995, 1997, 1999; Chilton, 1997; Abookire and Norcross, 1998). Two categories of tow depth (<40 m or ≥40 m) and three categories of sediment grain size (gravel, sand, or mud) were defined (e.g., Figure 1). Proportionally more fishes were examined for diet at habitats where those fishes were most abundant. Fifty-two percent of the fishes analyzed for diet were collected on shallow sand, and 3–14% of fishes were collected on other habitats.

Where five or fewer individuals of a size class of fish contained prey at a habitat, that habitat was omitted from analyses of diet for that fish size class. The small quantity of small (12–20 mm) yellowfin sole captured on any habitat (N<4) made it impractical to test for habitat related differences in the diet of this species size class, but sufficient quantities of larger juvenile yellowfin sole were available.

DATA ANALYSIS

Pooling of prey taxa

Two levels of taxonomic precision were used in dietary analyses. Prey taxa were pooled at broad taxonomic levels for certain analyses to reduce the number of prey categories and increase the sample size within a category. For example, amphipods of various species and families were combined into an "amphipods" category. Prey taxa that had been identified to a more precise taxonomic level (i.e., species, genus, or family) were pooled in the following categories: polychaetes, mollusks, copepods, krill, shrimp, crabs, cumaceans, isopods, amphipods, and fishes. Pooling prey at a broad taxonomic level assists with the summarization of prey taxa. Prey taxa were pooled in plots of proportional prey biomass and in statistical tests of prey presence/absence. However, pooling prey can result in loss of information (Rice, 1988), e.g., pooled prey allow a less precise measure of diet overlap than more precise taxonomy and may falsely inflate the estimates of competition between two predators over individual prey taxa. Therefore, cluster analyses, ordinations, and indices of diversity and

overlap were calculated using the most specific taxonomic information available. Except as noted, all statistical analyses were performed with Statistica software (StatSoft, 1995), and differences were considered significant where $p \leq 0.05$.

Division of flatfish species into size classes

Each fish was divided into groups (species size classes) using the separate but analogous methods of cluster analysis and ordination of prey biomass at increments of fish length. For each analysis, fish of a single species were divided into $\geq$5 mm length increments, with bin size set to a lower threshold quantity of eight fish. Where N<8 fish occurred within a 5 mm length increment, each fish in that increment was assigned to the next larger or smaller increment of closest total length. Proportional biomass contributed by each prey taxon, identified to the most precise level, was calculated for individual fish. The proportional contribution of each prey taxon was summed over each fish within the particular length increment, and the summed data were square root transformed and standardized to 100% over each fish length increment.

A Bray–Curtis dissimilarity index was calculated from the transformed, standardized data and used in cluster analyses to group fish of similar dietary composition. The amalgamation rule was set to Ward's (1963) method, which uses analysis of variance to evaluate the distance between clusters. Intraspecific length

groups were divided at major break points in each dietary cluster diagram, similar to the methods used by Stehlik and Meise (2000).

Principal components analysis (PCA) was performed to quantify dietary differences among fish length increments. The standardized data used in cluster analyses were not transformed for PCA analysis. Removal of less-common prey (i.e., prey taxa consumed by a single fish length increment) did not substantially reduce the amount of variation described by the first two axes, and therefore all prey taxa were retained for PCA. Where results of PCA and cluster analysis did not support each other, the grouping indicated by PCA was used in further size-related diet analyses.

Analyses of species size class abundances and diets

Abundances of fish at each collection site were standardized to density (number of fish per 100 m^2 area trawled), an improvement over the prior calculations of abundance based on amount of time towed (e.g., Norcross *et al.*, 1993, 1995, 1997). Tow area was calculated by multiplying the effective net swath of 2.7 m (Gunderson and Ellis, 1986) by the distance towed. Where available, tow distance was calculated from standard GPS coordinates obtained at the beginning and end of each tow. A majority of tows in Chiniak Bay did not have available GPS coordinates; distances for these tows were estimated using least trimmed squares robust regression (S-Plus, 1993) of GPS distance towed per minute aboard the same vessel used in 1991 (Dressel and Norcross, 1998). To reduce the impact of

large catches on statistical comparisons, values of density were log-transformed (log [(number of fish per 100 m^2) +1]). Abundances of individual species size classes were compared among habitats, using one-way ANOVA followed by Tukey HSD for unequal N. Length of fish within a species size class also was tested between habitats by Tukey HSD for unequal N.

Diet indices included an index of vacuity, proportional fullness, diet diversity, and diet overlap. The index of vacuity examines the number of stomachs that are empty relative to those which contain food.

$$\text{Vacuity} = (N_E / N_T),$$

where the number of empty stomachs is represented by N_E, the total number of fish examined is N_T, and vacuity is presented as a percentage. A value of proportional stomach fullness was recorded during laboratory analysis as described previously (page 7). Diet diversity was analyzed with the Shannon–Wiener index (Smith, 1986) and was based on the most precise level of prey taxonomy available, i.e., data were not pooled. Higher numbers indicate greater diversity of diet.

$$H' = -\Sigma_i p_i(\log p_i),$$

H' = diet diversity, and p_i = the proportion of the total biomass arising from the i^{th} species of prey. The Tukey HSD test for unequal N was used to detect differences between species size classes within indices of vacuity, observed

fullness of fish stomachs, and diet diversity. Schoener's (1970) index was used to quantify dietary overlap between species size classes, and like the diet diversity index, dietary overlap was based on the most precise level of prey taxonomy available. This index is recommended for diet studies that lack resource availability data (Wallace, 1981), and is expected to be accurate for most of the potential overlap range (Linton *et al.*, 1981). To ensure each fish within a species size class was weighted equally, the proportional biomass contributed by a prey taxon to each fish was calculated. The proportional biomass provided to a species size class was then calculated over all sites and within each habitat. The potential range of Schoener's Index was from 0 to 1, and values were presented as percentages. A value of 0% would indicate no prey taxon was consumed by both species size classes, and a value of 100% would represent complete diet overlap, in which all prey taxa provided equal proportions of biomass to both predators.

$$\text{Diet overlap} = 1 - 0.5 * \sum |P_{Xi} - P_{Yi}|,$$

The proportional weights of prey i in the diets of species x and y are given by P_{xi} and P_{yi} , respectively.

Prey taxon availability and use

No direct measures of prey availability are presented. Although infauna was collected with sediment samples, few of the taxa found in juvenile flatfish diets

were observed in the benthic infauna (Holladay, unpublished data). In Cook Inlet, south-central Alaska, efforts to assess abundance of fauna eaten by yellowfin sole were similarly unsuccessful, although a variety of gear was employed to collect fauna from within and near the bottom (Feder *et al.,* 1981). Even if measures of absolute abundance of infauna and epifauna had been accessible, without knowledge of the size range and ecology of prey taxa, absolute abundance is a less than perfect assessment of the availability of prey that a particular species and size of flatfish can catch, consume, and digest.

A proxy for prey availability was assessed by examining the proportional frequency of occurrence a prey taxon appeared in the diet of juvenile flatfishes, a method similar to one which used stomachs of Pacific halibut to sample the availability of forage fishes (Roseneau and Byrd, 1997). Prey taxa were pooled, and frequency of occurrence (FO) was calculated separately for each species size class on each habitat.

FO = (number of fish containing prey taxon / number of non-empty fish). This indirect assessment of prey availability indicated only where prey taxa were present relative to depth–sediment habitat. Thus, the proxy did not provide conclusive evidence of prey absence or abundance among habitats or patchiness of prey abundance and distribution within a habitat. This proxy does not necessarily account for possible dietary selectivity.

Differences in use of prey by groups of fishes were assessed by the non-parametric Friedman ANOVA test. Prey eaten by individual fish were pooled into taxonomic groups and converted to presence/absence data to test for dietary differences among groups of fish. The presence/absence datum consisted of an indicator variable designated as one if a prey taxon was present and zero otherwise. When less than six individuals of one species size class on a habitat contained prey, that group of fish was omitted from diet-by-habitat analyses to reduce likelihood of Type I errors. The frequency of occurrence of a prey taxon within a group of non-empty fish was ranked and then tested for differences by Friedman ANOVA. This test was performed among species size classes caught on a single habitat, and among habitats for a single species size class.

RESULTS

DIET OF EACH SPECIES, WITHOUT CONSIDERATION OF HABITAT

Flathead sole, Pacific halibut, rock sole, and yellowfin sole each ate a variety of crustaceans, polychaetes, mollusks, and fishes (Table 1). Crustaceans were the most commonly utilized prey by each flatfish species in terms of both presence (Table 1) and proportional biomass (Figure 3). Crustacean taxa eaten by each of the four species, in overall order of presence in flatfish diets, were amphipods, copepods, cumaceans, opossum shrimps (mysids), ostracods, shrimp, crabs, isopods, and krill (Table 1). Most prey were consumed whole, without being

masticated or torn. Notable exceptions were polychaetes and bivalves. Flatfishes of each species usually ate either heads or tails of polychaetes rather than eating the entire worm, and flathead sole, rock sole, and yellowfin sole ate bivalve siphons.

Flathead sole ate mollusks, amphipods, mysids, and shrimp (Figure 3a). Flathead sole smaller than 49 mm ate mainly amphipods. Mysids and shrimp provided most of prey biomass (combined biomass of 45–100%) to flathead sole larger than 60 mm. The two smallest length increments of flathead sole (20–29 and 30–39 mm) ate similar proportions of prey taxa, and a single fish of 48 mm ate only amphipods. Most of the biomass of mollusks consumed by flathead sole smaller than 90 mm consisted of bivalve siphons. Larger fish ate more mollusks with shells, primarily bivalves. Arrow worms were eaten only by flathead sole larger than 70 mm.

Halibut mainly ate crustaceans, but prey taxa changed substantially with increasing fish length (Figure 3b). As with flathead sole, larger Pacific halibut fed increasingly on larger prey. The smallest length increment of halibut (30–39 mm) ate mainly cumaceans and amphipods. The next three larger 10 mm length increments of halibut (40–49, 50–59, and 60–69 mm) ate the same proportion of amphipods, but ate progressively less weight of cumaceans and more of mysids and shrimp. Shrimp were eaten by halibut over the entire length range of fish examined, but mysids were eaten only by halibut smaller than 79 mm, with the

exception of two fish within the 160–169 mm length increment. Halibut less than 50 mm ate crab zoeae, and only halibut larger than 90 mm ate epibenthic crabs. Amphipods composed a substantial part of ingested biomass only for halibut smaller than 100 mm, and fishes were eaten only by halibut larger than 100 mm.

Across the entire length range examined, rock sole consumed polychaetes, mollusks, mysids, amphipods, and cumaceans (Figure 3c). Polychaetes contributed approximately 20% to prey biomass of rock sole smaller than 80 mm and contributed a slightly higher proportion of biomass as fish size increased beyond 80 mm. Mollusks contributed less than 20% to prey biomass, except for a single fish of 150 mm, which ate mainly bivalve siphons. Mysids were eaten by rock sole smaller than 130 mm. Each 10 mm length increment of rock sole ate cumaceans, but this prey taxon provided $\geq$10% of prey biomass only to fish smaller than 120 mm. Amphipods contributed approximately 20% to prey biomass of rock sole at all 10 mm length increments, except for the length increments from 130 to 159 mm, which each involved only 1–2 fish. Copepods, primarily harpacticoid copepods, were eaten only by rock sole smaller than 60 mm. Crab zoeae were consumed by rock sole smaller than 115 mm, and epibenthic crabs were eaten by fish larger than 140 mm.

The diet of yellowfin sole, as with flathead sole and halibut, changed substantially from the smallest to the largest fish (Figure 3d). The smallest fish

ate very small crustaceans, larger fish ate increasingly larger crustaceans, and fish larger than 80 mm consumed primarily polychaetes and mollusks. Yellowfin sole smaller than 20 mm TL ate only ostracods and harpacticoid copepods, and three yellowfin sole of 20 mm TL ate only harpacticoid copepods (Figure 3d). The next largest fish examined were 35 and 40 mm. The fish of 35 mm ate shrimp and cumaceans. Fish larger than 40 mm ate polychaetes, mollusks, amphipods, and cumaceans in addition to copepods (both harpacticoid and calanoid) and ostracods. Copepods composed $\geq$10% of prey biomass for yellowfin sole smaller than 120 mm. Cumaceans contributed a small portion of prey biomass to nearly all length increments of yellowfin sole larger than 20 mm. Amphipods provided $\geq$10% of prey biomass for yellowfin sole 40–169 mm in length. Mollusks, including whole gastropods, whole bivalves, and bivalve siphons, were eaten by most of the fish larger than 80 mm. Polychaetes composed about 20% of prey biomass for yellowfin sole 40–109 mm in length, and as fish size increased, polychaetes generally contributed more to the diet.

Although each species primarily ate crustaceans, there were differences in the taxonomic composition of prey, both within and among species. The diet of each fish species changed with larger fish size (Figure 3). The progression of dietary habits as fish size increased was most apparent for flathead sole, halibut, and yellowfin sole. Rock sole evinced a less marked change in prey composition

with increased length of fish. The fish size at which dietary composition changed the most was different for the different flatfish species (Figure 3).

Division of species size classes

Size-class divisions of fish did not occur at the same lengths, nor was the same number of size classes indicated for each species (Figures 4–7). Using separate but complementary strategies of cluster analysis on transformed data of prey biomass and ordination on untransformed data, flathead sole and rock sole were divided into two size classes, and halibut and yellowfin sole were divided into three size classes. Within a single species, size class distinctions based on diet were often analogous to age class separations reported for these collections, which had been estimated primarily on fish length (Figure 8; after Norcross *et al.*, 1993, 1995). Divisions into dietary size classes occurred between age-0 and age-1 for flathead sole, Pacific halibut, and yellowfin sole. Additionally, Pacific halibut within the age-0 year class were divided into small and medium fish.

Size class separations for flathead sole and Pacific halibut were unambiguous. Flathead sole (Figure 4) were divided into small (26–48 mm, N=163) and large (61–168 mm, N=96) classes. A clear separation between the diets of small and large flathead sole was evident with cluster analysis (Figure 4a). The distinct difference between small and large flathead sole (Figure 4b) was also indicated by PCA ordination of prey biomass, with 89% of data variation

explained by the first two ordination axes. Small flathead sole were age-0, and large flathead sole included individuals of ages 1–2 (Figure 8).

Pacific halibut (Figure 5) were separated into small (35–49 mm, N=89), medium (50–75 mm, N=80), and large (94–190 mm, N=26) classes. More dissimilarity was detected using cluster analysis between small and large halibut than between small and medium halibut or between medium and large halibut (Figure 5a). Ordination by PCA of prey biomass over halibut length increments (Figure 5b) echoed the three discrete groups found by cluster analysis, with 66% of data variation explained by the first two ordination axes. Both small and medium Pacific halibut were within the age-0 year class, and large halibut were comprised of age-1 plus the smallest age-2 individuals (Figure 8).

Size classes of rock sole and yellowfin sole were less clearly separated than those of flathead sole and halibut. Rock sole were divided into two slightly different sets of smaller and larger individuals with cluster analysis (Figure 6a) and PCA ordination (Figure 6b). Dissimilarity within the cluster matrix separated smaller (20–59 mm) from larger (68–184 mm) rock sole (Figure 6a). However, PCA ordination of rock sole length increments distanced only 20–34 mm rock sole from all larger fish (Figure 6b). Because PCA ordination did not indicate a division of rock sole ≥35 mm into multiple size classes, subsequent analyses of rock sole diet used only two discrete size classes, i.e., 20–34 mm (N=361) and 35–184 mm (N=274),

with 69% of data variation explained by the first two ordination axes. Small rock sole were all age-0, and large rock sole included larger age-0 fish, age-1 fish, and a few of the smaller age-2 fish (Figure 8).

Yellowfin sole were divided into small (12–20 mm, N=9), medium (36–84 mm, N=180), and large (86–189 mm, N=71) size classes (Figure 7). Small and large yellowfin sole appeared to be more closely related than either size class was to the medium size class (Figure 7a). The same size classes suggested for yellowfin sole by cluster analysis were supported with PCA ordination (Figure 7b). Although the size classes of yellowfin sole detected using PCA ordination were discrete, they were neither as distant from each other nor as tightly grouped as those of flathead sole (Figure 4b) and halibut (Figure 5b). Sixty-three percent of data variation in yellowfin sole diet was explained by the first two ordination axes (Figure 7b). Small yellowfin sole were age-0, medium yellowfin sole were age-1, and large yellowfin sole included age 2 and the smaller age–3 fish (Figure 8).

Over all four species of flatfish, 87% of individuals contained prey in their stomachs. No medium halibut or small yellowfin sole had an empty stomach (Table 2). The proportion of empty stomachs was significantly different among the species size classes ($F=15.96$, $p<0.0001$). Within a species, the size classes generally were of statistically similar vacuity. Rock sole were an exception to this rule, as large rock sole were empty more often than small rock sole ($p\leq0.05$).

Across species, more flathead sole were empty, followed by yellowfin sole and halibut. Rock sole had the lowest proportion of empty stomachs.

The difference in proportional fullness among fishes containing prey was highly significant ($F=23.4$, $p<0.0001$), and significant differences in proportional fullness were detected between most pairs of species size classes (Table 3). Mean values of proportional fullness were nearly always similar among the size classes of one species. However, there were significant differences in proportional fullness between every pair of species. Halibut stomachs were most full (mean fullness of size classes = 75–83%), followed by rock sole (74–75%) and flathead sole (65%). Yellowfin sole stomachs were least full (37–54%).

There was a highly significant difference in diet diversity among all species size classes ($F=12.8$, $p<0.0001$). Small yellowfin sole and small flathead sole had the least diverse diets, and large yellowfin sole and large halibut had the most diverse diets (Table 4). Diversity of diet within a species was significantly greater for larger flathead sole, halibut, and yellowfin sole. Small and large rock sole had the same diversity of diet. The diet of small yellowfin sole was less diverse than that of each species size class except small flathead sole, and small and medium halibut. Additionally, the diets of medium halibut and small rock sole were less diverse than that of large yellowfin sole.

Dietary overlap of prey biomass between species size classes ranged from 0 to 66% (Table 5). Within a species, only small and large rock sole had a high

(>50%) diet overlap. Two other pairs of species size classes had high diet overlap, i.e., large flathead sole–medium halibut, and large rock sole–medium yellowfin sole. Medium (20–50%) dietary overlap was found between 66% of the 45 possible pairwise contrasts. The fishes having diets least like any others were small yellowfin sole (0–19% overlap with any other diet) and large Pacific halibut (0–28% overlap with any other diet).

Analyses considering Habitat

Fish abundance by habitat

The largest catches of small and large flathead sole were in deep areas of each substrate category, while the largest catches of other fishes were generally shallow and at sand and/or mud substrate (Table 6). All Pacific halibut were caught at shallow habitats, except for small halibut, which were also caught at deep sand. The largest catches of rock sole were at sand or mud in shallow water, except for one large catch of small rock sole caught on sand in deeper water. The largest catches of yellowfin sole were at sandy or muddy shallow sites.

Significant differences in abundance within one species size class were detected between habitats for each species size class except small, medium, and large halibut and small yellowfin sole (Table 6). Small and large flathead sole were caught in significantly greater abundance at sandy or muddy substrates in deep water, and also were caught in large numbers at one site within the deep gravel habitat. Small rock sole were caught in significantly greater abundance on shallow

sand in shallow areas, and were caught in large numbers at shallow mud and deep sand habitats. Medium yellowfin sole were captured in significantly greater abundance at shallow sites of sand or mud substrate, while large yellowfin sole were in significantly greater abundance only at shallow muddy sites.

Fish diet by habitat

Differences in vacuity, proportional fullness and diet diversity could be attributed to habitat for some species size classes (Table 7). The only species size class having a significant difference in index of vacuity among habitats was large flathead sole. However, index of vacuity for this fish was not significantly different between any two habitats ($p>0.1$). Within some depth–sediment habitats, small sample sizes limited the number of habitat comparisons. There were insufficient numbers of non-empty fish of any species size class to contrast diet across all six habitats. Two to five habitats were contrasted (Table 7).

Significant differences in proportional stomach fullness of fish containing prey were detected among habitats for each species size class except small flathead sole and medium Pacific halibut (Table 7). Large flathead sole were more full on deep sand (78±19%) than on deep mud (56±32%) ($p<0.05$). Small halibut were more full on deep sand (97±8%) than on shallow sand (72±28%) ($p<0.001$). Large halibut were more full at shallow gravel (83±20%) than shallow sand (63±21%) ($p<0.05$). Small rock sole were slightly more full on deep sand (81±24%) than on shallow sand (70%±25%) ($p<0.05$). Large rock

sole were more full on shallow sand (78±26%) than on shallow gravel (57±28%) ($p<0.01$). Although differences in proportional fullness among habitats were significant for both medium and large yellowfin sole (Table 7), no differences were detected between habitats for either medium ($p=0.08$) or large ($p=0.06$) yellowfin sole. Large rock sole were significantly more full and more abundant at shallow sand than shallow gravel. Habitats where large flathead sole, small and large halibut, and small rock sole were significantly less full were the same habitats where these species size classes were found in the highest abundance (Table 6). Relatively greater abundances of several species size classes were found at deep sand, a habitat where large flathead sole, small halibut, and small rock sole had significantly greater fullness.

Differences in diet diversity within a species size class could be attributed to habitat for small and large flathead sole, small and large halibut, and small rock sole (Table 7). The diversities of small flathead sole and small rock sole diets were significantly different over all habitats, but no significant differences were detected between any two habitats (small flathead sole: $p>0.06$; small rock sole: $p>0.1$). The diet diversity of large flathead sole was higher on deep gravel (0.79±0.31) than on shallow sand (0.45±0.35)($p<0.05$), and small halibut had a more diverse diet on shallow sand (0.50±0.43) than on deep sand (0.08±0.22) ($p<0.001$). The diet of large halibut was more diverse on shallow gravel (0.83±0.36) than on shallow sand (0.42±0.45) ($p<0.05$). Shallow sand habitat

was involved in each significant contrast of diet diversity; it was the habitat of lower diet diversity for large flathead sole and large halibut, and the habitat of higher diet diversity for small halibut.

Prey availability and use relative to habitat

Differences were observed in the proxy indices of prey availability at different habitats (Table 8) and the proportion of fish within different species size classes that consumed particular prey taxa (Table 9). Amphipods, copepods, mysids, polychaetes, and mollusks were eaten at each depth–sediment habitat, but only amphipods were eaten by ≥25% of a species size class at each habitat (Table 8). A relatively large variety of prey taxa was available at shallow gravel or sand habitat and at deep sand habitat, and the lowest variety of prey was at deep areas of gravel or mud substrate. Proportional frequency of occurrence (FO) values for isopods and krill were ≤25% at any habitat or within any species size class. Although individual fish within each species ate isopods and krill (Table 1), more small flathead sole, large rock sole, and medium yellowfin sole ate isopods than did other species size classes. More large rock sole and medium yellowfin sole ate krill than did other species size classes. Both isopods and krill were consumed at several habitats. In many cases, a prey taxon eaten by ≥25% of individuals of one species size class at one or more habitats was eaten by all size classes of that species (Table 9). Where FO of a prey taxon was ≥25% in either the smaller or larger size class of a fish species, generally small prey (i.e.,

copepods, cumaceans, ostracods) were eaten by small fish, and larger prey (i.e., shrimp, crabs, fishes) were eaten by larger fish. Copepods were eaten by small but not large flathead sole. Cumaceans and mysids were eaten by small and medium, but not by large, halibut. More medium and large halibut consumed shrimp and crabs, and fewer medium and large halibut consumed polychaetes, than did small halibut. Fishes were consumed only by large halibut. More small than large rock sole ate ostracods, and more large than small rock sole ate crabs. More large than small yellowfin sole ate mollusks. Apparent differences in prey availability among habitats, and prey consumption within a species of fish, did not effect significant differences in prey resource utilization among species size classes examined from within one habitat ($\chi^2<11.6$, $p>0.1$; Table 10).

Diets of species size classes were tested across habitats, and seven of the nine species size classes exhibited statistically similar prey composition across habitats (Table 11). Small Pacific halibut and small rock sole, but no other species size class, had significantly different prey FO at different habitats. Prey taxon FO within small halibut was significantly different between shallow and deep sandy sites ($\chi^2=6.4$, $p=0.01$), but not between shallow gravelly sites and either shallow sandy or deep sandy sites ($\chi^2=0.0–3.6$, $p=0.06–1.0$). Small rock sole exhibited significantly different prey use ($\chi^2=4.5–7.4$, $p=0.01–0.03$) between the following pairs of habitats: shallow mud–shallow gravel; shallow mud–shallow sand;

shallow sand–deep sand; shallow sand–deep mud. To explain the significant differences in prey consumed among habitats occupied by small Pacific halibut or small rock sole (Table 11), the prey FO was evaluated for each of these fishes at individual habitats (Table 12).

No prey taxon was eaten at each habitat by >25% of small halibut (Table 12). At shallow gravel habitat, most (58–79% of fish) halibut ate cumaceans and amphipods; at shallow sand habitat, most small halibut (60% of fish) ate amphipods, and at deep sand habitat, all small halibut ate cumaceans. Polychaetes, copepods, mysids, and shrimp were eaten by other flatfishes at habitats where small halibut did not eat them. Polychaetes were eaten by small halibut only at shallow gravel habitat, while copepods, mysids, and shrimp were eaten by small halibut mainly at shallow sandy sites. The size of the small halibut containing prey was largest at shallow gravel, smaller at shallow sand, and smallest at deep sand. The size difference was significant between fish at shallow gravel and deep sand ($p<0.001$).

At each habitat except deep sand, most (56–90%) small rock sole ate copepods. Most (52–67%) small rock sole also ate mysids at shallow gravel, polychaetes at shallow mud, and mollusks at deep mud. Like the small halibut examined from deep sand, most (51%) small rock sole at this habitat ate cumaceans. Each prey taxon eaten by $\geq$25% of small rock sole (Table 9) at any habitat was consumed by a similar proportion ($\geq$25% FO in at least one species

size class) of fish at shallow gravel, shallow sand, and deep sand (Table 8), but ostracods were not eaten at deep mud habitat. Small rock sole took prey from each of the taxa observed in the stomachs of any fish species at shallow sand (18–79%). Prey taxa eaten by small rock sole on some, but not all, habitats where the prey taxon was available included cumaceans, mysids, polychaetes, and mollusks. As observed for small halibut, the size of small rock sole decreased across habitats, with the largest fish examined from shallow gravel and the smallest fish examined at deep mud. Small rock sole were significantly larger at shallow gravel and shallow sand than at deep sand ($p<0.05$).

Significant differences in proportional fullness (Table 13) and diet diversity (Table 14) within one flatfish species were sometimes attributed to size class, sometimes attributed to habitat, and sometimes to the interaction of size class and habitat. Analyses of one flatfish species over all habitats (Table 3) detected differences in proportional stomach fullness only between medium and large yellowfin sole, a difference which could be partially attributed to the interaction of fish size and habitat (Table 13). Habitat and proportional fullness were correlated for halibut and rock sole. The interaction of habitat with size class was the factor most highly correlated with rock sole proportional fullness. Diet diversity was significantly correlated with size class within each species except rock sole (Table 14). Habitat was significantly correlated with diet diversity of each of the four flatfish species. The interaction of habitat with size class was significant for diet

diversity of flathead sole and halibut. Size class was the most highly correlated factor affecting dietary diversity in flathead sole and yellowfin sole, while habitat was the most highly correlated factor for halibut and rock sole.

DISCUSSION

ONTOGENETIC SHIFTS IN DIET

In the present study, juvenile flathead sole, halibut, rock sole, and yellowfin sole primarily ate small crustaceans near Kodiak Island during summer, as they do in other regions during summer (e.g., Sturdevant, 1987) and other seasons (McGregor, 1990; Holladay *et al.*, 1999). Diets of juvenile flatfishes in Kodiak Island nursery areas varied with species and size of fish within each species. Most size classes examined of these fishes ate crustaceans. Generally, smaller taxa are eaten by small fishes and larger crustaceans and non-crustacean taxa are eaten by larger fishes. Within a species, the diets of larger juvenile fish resemble the diets of adults more closely than diets of smaller juveniles do.

Size-related variations in dietary composition of these flatfishes are observed in other regions of the northwest Pacific and Alaska in addition to Kodiak Island. Since fish size and regional diet are potentially confounding parameters, details of diet relative to fish size from other regions are combined below with results of the present study to provide a more complete review of diet over the juvenile–early adult age range than has previously been reported for these species. It is important

to note that, although a wide range of depths and sediment grain sizes were examined in dietary analyses at Kodiak Island (this study) and Kachemak Bay (Holladay, *et al.*, 1999), this was not always the case in other regions. For example, halibut from Auke Bay, southeastern Alaska, were collected only close to shore, at a 16 m area with fine sand and mud substrate (Sturdevant, 1987), and rock sole and yellowfin sole from Auke Bay were caught intertidally on muddy substrate (McGregor, 1990).

Newly settled flathead sole (20–29 mm) near Kodiak ate amphipods and other small crustaceans, while flathead sole larger than 60 mm ate proportionally fewer small crustaceans and more decapod crustaceans such as mysids and shrimp. An ontogenetic shift in the summer diet of flathead sole is also apparent at 60 mm length in Kachemak Bay, Cook Inlet, Alaska (Holladay and Norcross, unpublished data). In research in Kachemak Bay which did not differentiate among winter, spring, or summer collections, more smaller juvenile flathead sole (28–51 mm) eat copepods and more larger (52–165 mm) flathead sole eat shrimp (Holladay *et al.* (1999). In the present research and along the Washington coast (Miller, 1970; Pacunski *et al.*, 1998), juvenile flathead sole eat more mysids and shrimp as fish size increases. In the eastern Bering Sea, larger adult flathead sole generally eat larger prey than smaller adults (Smith *et al.*, 1978; Lang, 1992).

Size-related variation in the diet of Pacific halibut is well documented in Alaskan waters. Analysis of age-0 halibut near Kodiak found that newly settled

halibut (30–39 mm) primarily ate cumaceans, and as fish size increased, age-0 halibut ate more amphipods, shrimp, and mysids. In particular, at a size of 46–55 mm, Pacific halibut abruptly shift their primary diet source from cumaceans to mysids (Holladay and Norcross, 1995). This shift in prey accounts for the division of age-0 halibut by this study into small and medium size classes at 50 mm. In Auke Bay, halibut of 43–53 mm SL eat approximately equal amounts of amphipods, shrimp, and harpacticoid copepods (Sturdevant, 1987). This apparent regional difference in prey composition is likely due to differences between areas in size of fish and habitat. The size of fish examined in Auke Bay is near the size range at which the diet of age-0 halibut changes most (Holladay and Norcross, 1995). Additionally, the present study examined subtidal areas at various depths and sediment types, while Auke Bay collections were at a subtidal area shallower than 16 m having fine sand or silt sediments (Sturdevant, 1987). Larger juvenile halibut eat increasingly larger crustaceans (e.g., shrimp and crabs) and fishes (Hardman and Southward, 1957; Best and Hardman, 1982; Best and St-Pierre, 1986; this study). Adult halibut in Alaskan waters feed mainly on crabs, demersal fishes, and pelagic fishes (e.g., Feder and Jewett, 1981; Chilton *et al.*, 1995; Best and St-Pierre, 1986; Yang, 1995).

Near Kodiak (present study) and Auke Bay (McGregor, 1990), juvenile rock sole smaller than 35 mm have slightly different diets than larger fish. Juvenile rock sole ate a variety of small crustaceans near Kodiak; more fish smaller than 35 mm

TL ate ostracods, and more fish larger than 35 mm TL ate crabs (e.g., Figure 3c, Table 9). In Auke Bay, rock sole of 13–34 mm SL mainly eat harpacticoid copepods, and fish of 35–80 mm SL primarily eat bivalve siphons (McGregor, 1990). Again, the difference in dietary composition between Auke Bay and Kodiak is due in part to the limited range of habitat examined in Auke Bay and the dissimilarity of habitats between the two regions. In Auke Bay, rock sole were collected only in the intertidal zone over muddy sediment (McGregor, 1990). Larger juvenile (present study) and adult (Feder and Jewett, 1981; Lang, 1992) rock sole primarily eat polychaetes and crustaceans. Adult rock sole additionally eat mollusks in Cook Inlet (Feder *et al.*, 1981), and eat brittlestars (Feder and Jewett, 1981; Lang, 1992) and cannibalize other rock sole (Smith *et al.*, 1978) in the eastern Bering Sea.

At both Kodiak and Auke Bay, yellowfin sole undergo an ontogenetic change in diet at a size between 20 and 35 mm. Near Kodiak, small yellowfin sole (12–20 mm) ate ostracods and harpacticoid copepods. In Auke Bay, yellowfin sole of this size eat harpacticoid copepods almost exclusively (McGregor, 1990). In Auke Bay, yellowfin sole add polychaetes to their diet within the size range of fish missing from Kodiak samples, i.e., 21–34 mm (McGregor, 1990). In Kodiak, yellowfin sole slightly larger than 35 mm ate amphipods and both harpacticoid and calanoid copepods, and as fish size increased, juvenile yellowfin sole ate progressively fewer small crustaceans and more polychaetes and mollusks, i.e., whole animals of both

taxa, polychaete heads, and bivalve siphons. In Auke Bay, yellowfin sole within the medium size of this study (35–84 mm) eat calanoid copepods, polychaetes, and bivalve siphons during summer (Sturdevant, 1987), and bivalve siphons and harpacticoid copepods when examined over all seasons (McGregor, 1990). Near Kodiak, although yellowfin sole did not eat bivalve siphons until 55 mm in length, bivalve siphons were eaten by other fishes at the habitats where smaller fish yellowfin sole were found. As bivalve siphons and polychaete fragments were not identified to species, it is not clear if the same species of prey were present in both regions. Adult yellowfin sole in the eastern Bering Sea consume clams, gammarid amphipods, and polychaetes, and a slight decrease in gammarid amphipod predation is observed as size of adult yellowfin sole increases (Feder and Jewett, 1981; Lang, 1992).

Ontogenetic changes in diet occur at consistent sizes within the juveniles of a single flatfish species, although there are regional differences in dietary composition. That similar size-class divisions of diet are observed at three geographically separate regions, i.e., Kodiak Island, Kachemak Bay, and Auke Bay, and at different depths, i.e., subtidal versus intertidal, is strong evidence that these diet shifts reflect ontogenetic changes in the ability of these fishes to capture prey.

CONCURRENT ASSESSMENT OF FLATFISH AND PREY DISTRIBUTION

Collections of this study were made within a two-week span of time in order to minimize potential seasonal effects on flatfish abundance and diet. Collections were

in late summer, when most age-0 fishes are expected to have settled (Matarese *et al.*, 1989). This expectation was met by flathead sole and Pacific halibut; the smallest individuals of these species were several mm larger than size at transformation. Flathead sole transformation is probably gradual, beginning at 18-21 mm standard length (SL), while halibut transform at 15–25 mm SL and settle at 30 mm SL (Matarese *et al.*, 1989). However, the smallest rock sole (20 mm TL) and yellowfin sole (12 mm TL) caught by this study were close to expected transformation lengths, i.e., 18 mm SL for rock sole (Ahlstrom *et al.*, 1984), and 15–17 mm SL for yellowfin sole (Matarese et al., 1989). This indicates that the age-0 year classes of rock sole and yellowfin sole had not completely settled when samples were collected for this study. Late settlement may have affected abundance in this study, as shown by large collections of smaller rock sole in Sitkinak Strait, southern Kodiak, near the end of chronological sampling (Norcross *et al.*, 1995).

The dietary indices and proxies for prey availability presented in this study should be interpreted with caution because of their inherent limitations. The quantity and quality of samples and potential dietary selectivity by flatfishes affect each index and the proxy. Site-specific differences, such as localized patchy prey distribution and abundance, and the number of separate sites available or examined within a habitat also have an effect. Habitats near Kodiak contain small-scale spatial variations in habitat that have been observed to affect

the distribution of juvenile flatfishes and benthic macrofauna (Norcross and Mueter, 1999).

Dietary selectivity and the size of prey are parameters expected to have large influences on dietary diversity and prey availability, but they were not quantified by this study. The taxonomic level of prey identification is an additional factor that is noted but not considered here. Although prey were identified to species where practical, damaged or juvenile individuals and fragments were usually not identifiable to species. Dietary diversity in this study considered the most precise taxonomy available, while the proxy of prey availability used broad taxonomic categories.

Prey selectivity has been detected in postmetamorphic flatfishes in Auke Bay. At one intertidal, muddy site, the diets of flatfishes and availability of infaunal prey were examined for age-0 rock sole, yellowfin sole (Sturdevant, 1987; McGregor, 1990), and starry flounder (McCall, 1992). Initial identification of harpacticoid copepods to a broad taxonomic level led McGregor (1990) to conclude that timing of flatfish settlement is not concurrent with the highest seasonal density of their primary prey. However, this conclusion was revised by McCall (1992). Identification of McGregor's samples to greater taxonomic precision revealed that some juvenile flatfishes are highly selective for particular species of harpacticoid copepods (McCall, 1992). Timing of settlement and diet of the fish are correlated to a limited group of harpacticoid copepods rather than

all species available to newly settled flatfishes. In addition to different species, different sizes of individuals within a species may be selected. For example, one fish may not distinguish among the relative sizes of prey consumed, while another may be limited to consuming multiple prey species of similar size (Labropoulou and Eleftheriou, 1997). Arguably, the two fishes probably are not equipped to eat the same prey.

Little is known about dietary composition relative to prey availability of juvenile flatfishes within Alaskan waters. It is extremely difficult to collect benthic, epibenthic, and planktonic species that potentially are available as prey for flatfishes (Howard Feder, Institute of Marine Science, University of Alaska Fairbanks, personal communication). Costs of using a variety of collection methods in the field followed by intensive taxonomy of microscopic prey are prohibitive for large geographic areas such as Kodiak. Due to this scarcity of data, the summarization by this study of prey presence relative to depth–sediment habitats is particularly useful as a record of taxon presence, although absence and abundance of prey are not assessed. However, it is reasonable to assume that, in a habitat where a large number of fish within one species size class consume a prey taxon, then that prey taxon is sufficiently available for other fishes to consume. Thus, if a large proportion of one fish species consumes a prey taxon on a habitat, and other fishes on that habitat do not consume it, prey selectivity is suggested.

Depth and sediment, often in conjunction with size of fish, are known to influence distribution and feeding habits of other flatfishes, as well as those of this study. Depth and sediment influence the distribution of juvenile and adult Dover sole (*Microstomus pacificus*) and their prey, with depth having a stronger influence on distribution than sediment type (Pearcy and Hancock, 1978). Depth and fish size accounted for 85% of variation in diet of Greenland halibut (*Reinhardtius hippoglossoides*); as the fish grow, they move into deeper water where prey availability is expected to be different (Orr and Bowering, 1997). The diet of juvenile yellowtail flounder (*Pleuronectes ferrugineus*) varies more strongly with depth than with temperature (Langton, 1983). Under laboratory conditions, with equal prey availability across all sediment types, juvenile halibut, rock sole, and yellowfin sole choose sandy or muddy sediments (Moles and Norcross, 1995), as they did *in situ* (this study). In the present study, most prey taxa were eaten by one or more species size classes across all habitats. Food habits of adult flathead sole, rock sole, and yellowfin sole are correlated with sediment type in the eastern Bering Sea, where apparent sediment preference is inferred to be due to prey availability (McConnaughey and Smith, 2000).

Preference for habitat, inferred where significantly greater abundance of a species size class was caught at a depth—sediment category, did not appear to be related to differences in amount of food available or the presence of a particular prey taxon. No fish had significantly different vacuity between two

habitats, indicating that prey species were present within each of the habitats at which the species size class was caught. Although several fishes had differences in proportional fullness relative to habitat, usually a species size class was less full at its preferred habitat. This suggests that fishes are not choosing habitat based primarily on access to a particularly abundant food source. The taxa most consumed by juvenile flatfishes (e.g., amphipods, mysids, shrimp, cumaceans, polychaetes, and mollusks) each were present within most of the six depth–sediment habitats of this study. This finding supports the hypothesis that juvenile flatfishes are less food-limited at high latitudes (Miller *et al.*, 1991; Pauly, 1994). As noted previously, an issue that cannot be addressed by this research is the relative abundance of various prey taxa at a habitat. It is possible that either prey taxa were available but not consumed by the examined fishes, or that consumption of particular prey at a habitat is due to relative prey abundance or prey preference. This research argues that if one size class of fish eats a prey taxon at the habitat, the prey is "available" to all species size classes at that habitat. If this assumption is accepted, then if a prey is available but rarely or never eaten by a species size class, the prey taxon is not preferred by that fish.

The potential for competitive interactions within and between species of flatfishes is reduced somewhat near Kodiak by spatial partitioning of the habitat (e.g., Table 6). Juvenile halibut, rock sole, and yellowfin sole were caught in high abundance at similar depth–sediment habitats near Kodiak, i.e., shallow sandy

and muddy areas. Small rock sole were abundant at deep sandy areas as well as at shallow sandy and muddy areas where larger juvenile rock sole were abundant. Medium yellowfin sole were abundant in sandy or muddy shallow areas, and large yellowfin sole were in high abundance only in muddy shallow areas. Similar differences in habitat use by smaller versus larger individuals also are found along the Alaska Peninsula (Norcross *et al.*, 1999) and in lower Cook Inlet (Abookire and Norcross, 1998).

Adults of the flatfish species rock sole, yellowfin sole, and Alaska plaice (*Pleuronectes quadrituberculatus*) are common in the Bering Sea. The diets of these species were less similar in areas of known distributional overlap (Lang, 1992). Competition for food and habitat among juvenile rock sole can result in density dependence in Hecate Strait, but in the Bering Sea, juvenile rock sole are not expected to be density dependent, due to latitudinal differences in species distribution (Fargo and Wilderbuer, 2000).

Competition for prey can be an important factor in areas where food is limited. However, the index of vacuity examined here was similar across all habitats for a species size class, i.e., a single species size class was not empty more often on any habitat where it was examined. This indicates that prey of some type were consumed across the habitats at which flatfishes are found. Most prey taxa, at least when considering a broad level of identification as is presented here, were found at several habitats near Kodiak Island. Prey

composition was statistically similar among flatfish species caught at a single habitat. This finding supports the concept that these juvenile flatfishes usually feed opportunistically. Juvenile flatfishes coexisting in shallow fine-grained habitats of the study region did not appear to be food-limited, as assessed by stomach fullness and vacuity indices. In the present study, fish abundance did not appear to be limited by presence of prey taxa that these juvenile flatfishes could consume. The flatfishes were able to catch and consume many of the same prey taxa, and nearly all the pooled prey taxa were available at all habitats. This study does not indicate that competition for prey was a strong influence among juvenile flatfishes. Similarly, in the eastern Bering Sea, competition with other flatfishes for prey does not determine the diet of adult flathead sole (Pacunski *et al.*, 1998).

Potential for competition interactions among the newly settled juvenile flatfishes, which all ate small crustaceans, was reduced in part by different habitat preferences. These four juvenile flatfishes are found within a broad range of depth–sediment habitats (e.g., Norcross *et al.*, 1999; Figure 1). However, within a region a flatfish species usually is abundant only at a limited range of habitats. Relatively large catches of small halibut and small rock sole were taken outside the 'preferred' habitat, at deep sand. That these large catches may be associated with diets is a possibility supported by the high stomach fullness of large flathead sole, small halibut, and small rock sole collected on deep sand

habitat. However, there are many possible causes of differences in stomach fullness, including differential feeding intensity and gut evacuation.

This research does not indicate a strong association of abundance of any one of the juvenile flatfish species with the presence of a particular prey taxon. It is possible that a more precise taxonomic analysis of prey could produce conflicting results, as in Auke Bay (McGregor, 1990; McCall, 1992). Small juveniles of flathead sole, Pacific halibut, rock sole, and yellowfin sole were opportunistic feeders on small crustaceans, and increasingly larger juvenile fishes ate larger prey. When considered jointly with patterns of flatfish abundance, proportional stomach fullness, and prey taxon presence, our results do not indicate that prey dictated which habitats juvenile flatfishes selected.

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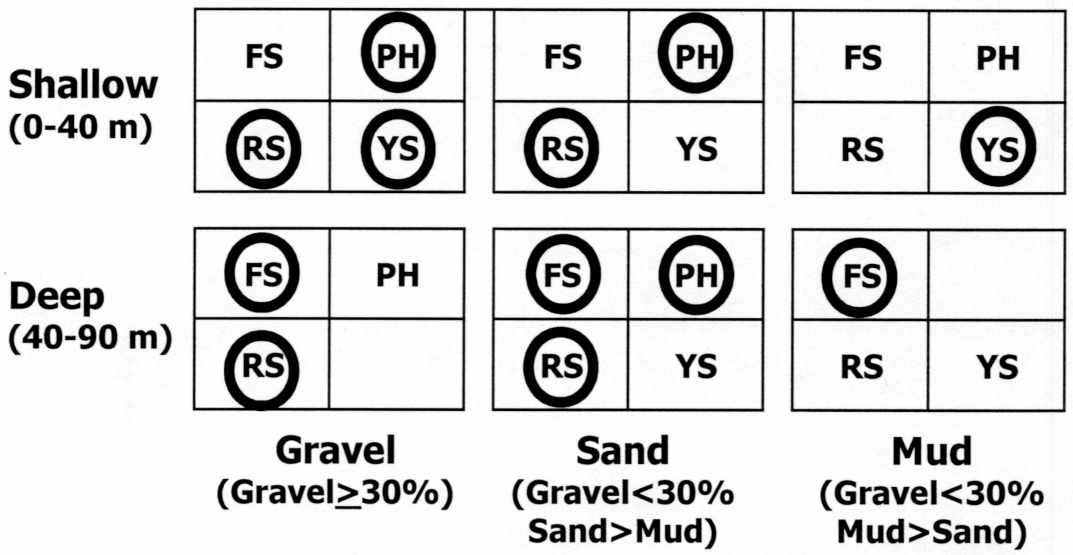


Figure 1. Presence and abundance of juvenile flatfishes at depth-sediment habitats in south-central Alaska. Summary of regional results for age-0 or age-1 fish from Kodiak Island (Norcross et al., 1993, 1994, 1995, 1997; Chilton, 1997), the Alaska Peninsula (Norcross et al., 1999), and lower Cook Inlet (Abookire and Norcross, 1998). Species presence is noted by abbreviated species name (flathead sole = FS, Pacific halibut = PH, rock sole = RS, yellowfin sole = YS). Circled abbreviations indicate higher abundance at this habitat within one or more studies of south-central Alaska.

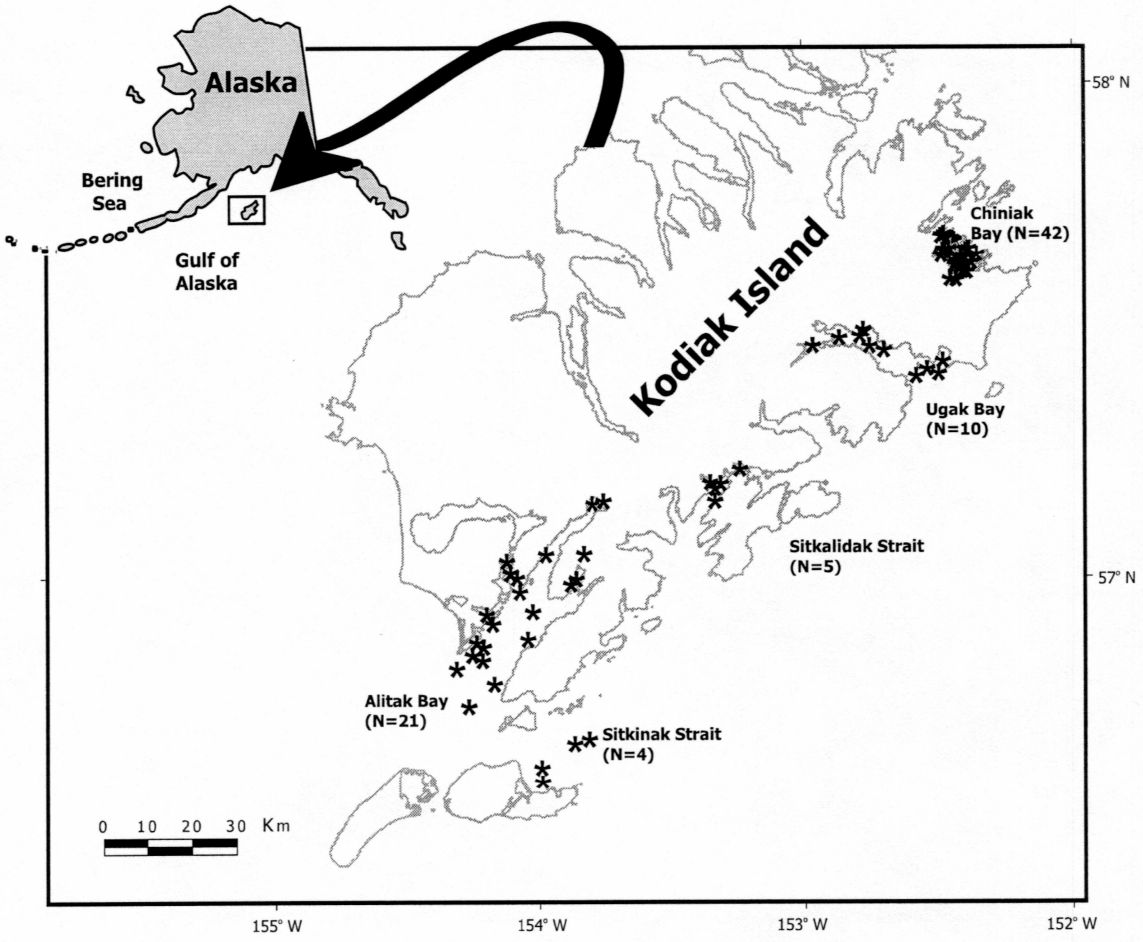
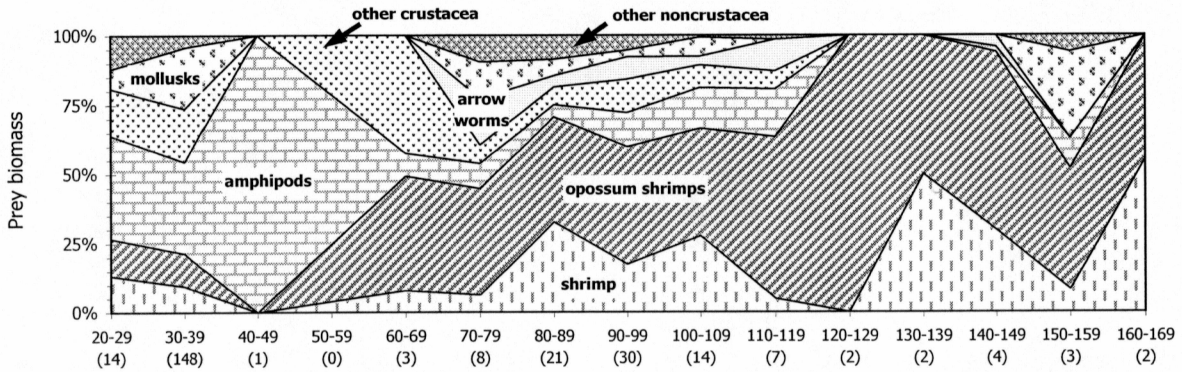


Figure 2. Sites to the east and south of Kodiak Island, in the northern Gulf of Alaska, where samples were collected. N=number of sites.

3a) Flathead sole (N=259)



3b) Pacific halibut (N=195)

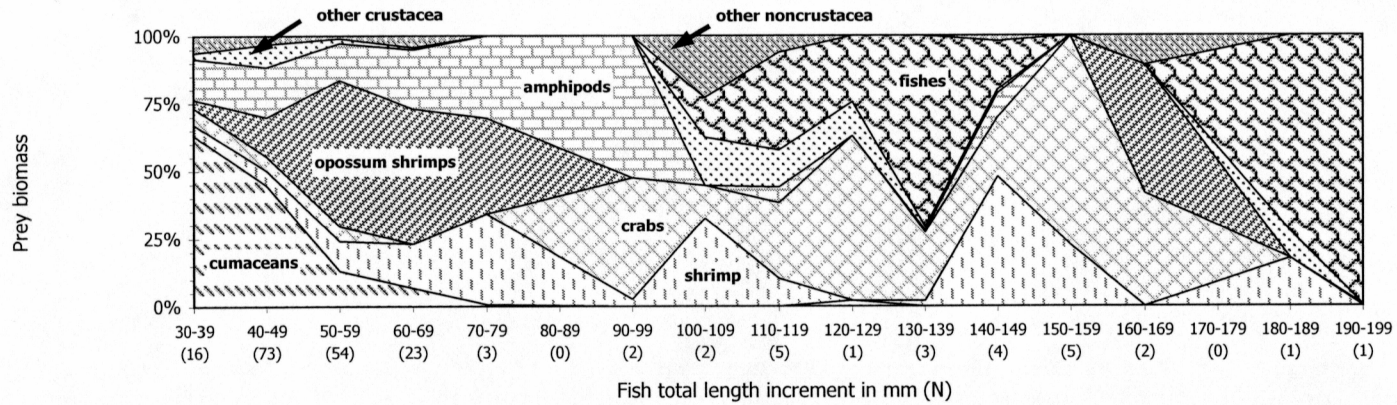
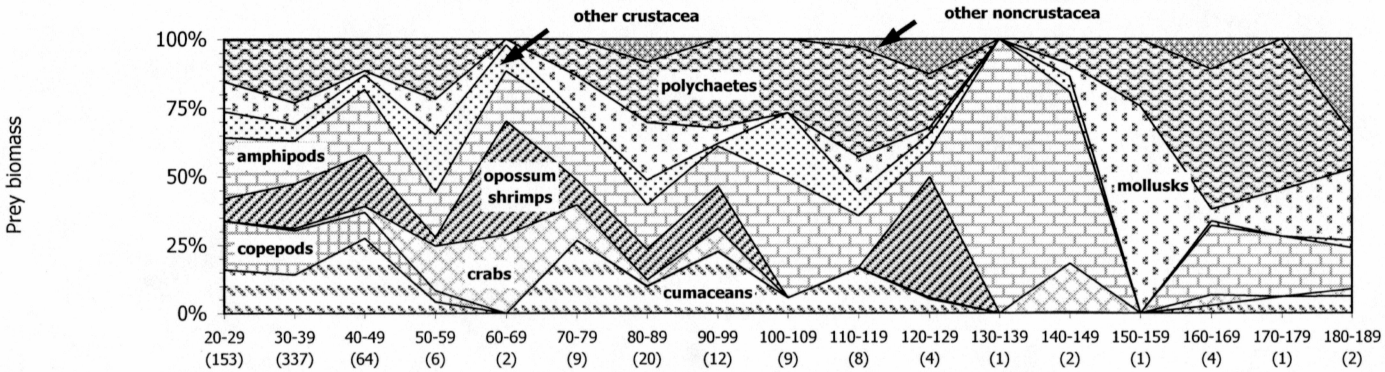


Figure 3. Proportional prey biomass for a) flathead sole and b) Pacific halibut, examined by 10 mm increment of fish length. The "other crustacean" and "other noncrustacea" categories include taxonomic families which contributed <10% to prey biomass at any length increment. Diet composition of each species is presented along a standard x-axis of fish size to facilitate interspecific contrasts among like sizes of fish.

3c) Rock sole (N=635)



3d) Yellowfin sole (N=260)

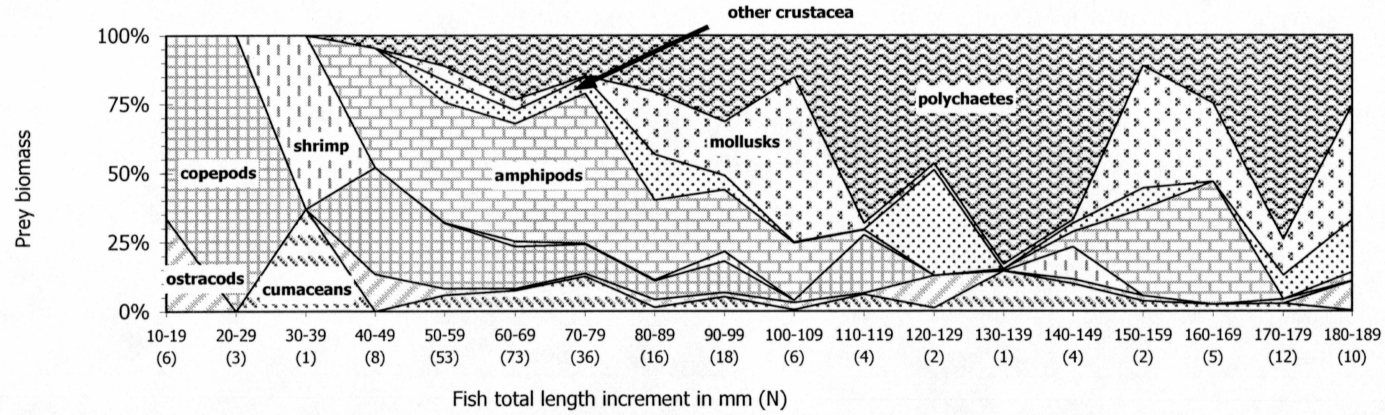
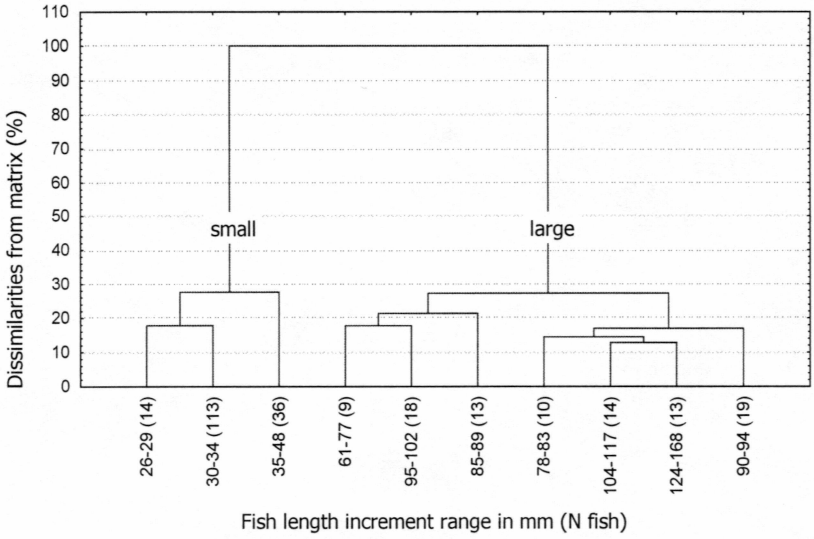


Figure 3. Proportional prey biomass for c) rock sole and d) yellowfin sole, examined by 10 mm increment of fish length. The "other crustaceans" and "other noncrustaceans" categories include taxonomic families which contributed <10% to prey biomass at any length increment. Diet composition of each species is presented along a standard x-axis of fish size to facilitate interspecific contrasts among like sizes of fish.

4a) Cluster analysis



4b) Principal components analysis

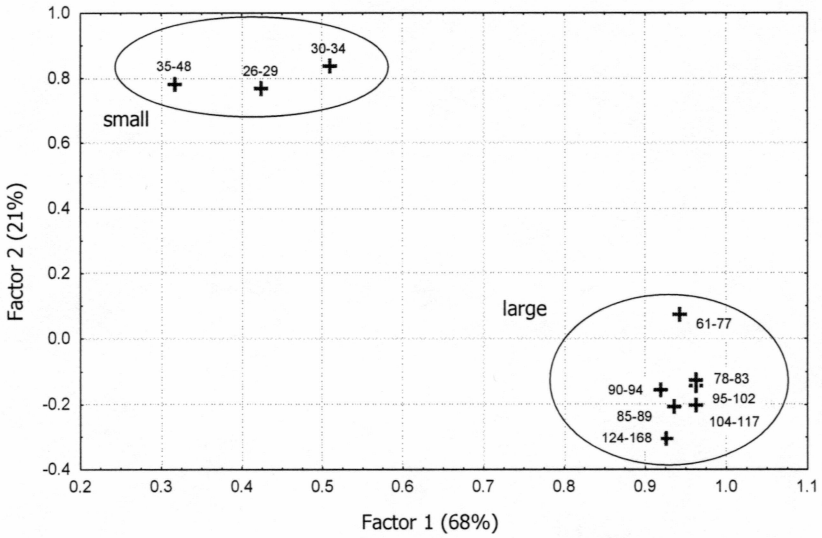
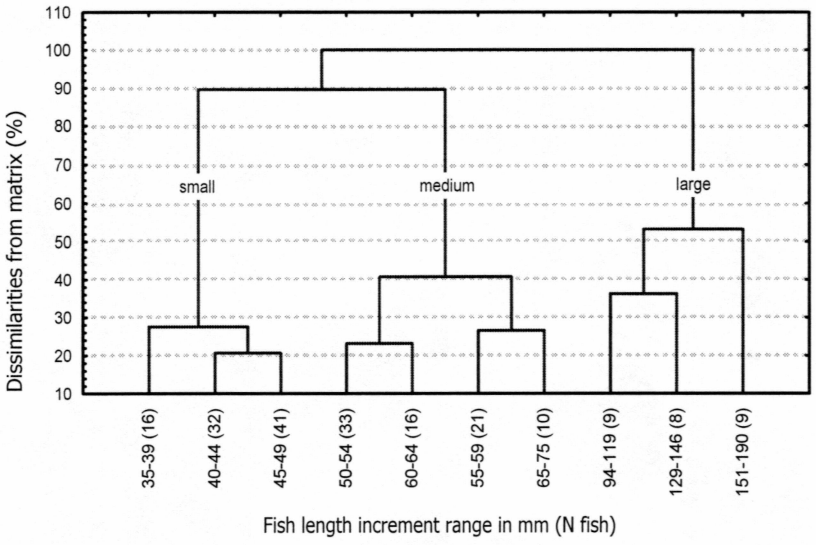


Figure 4. Analysis of flathead sole diet by fish length, using a) cluster analysis and b) principal components analysis.

4a) Y-axis distances reflect differences between proportional prey biomass indices at increments of fish total length; data are pooled over all predators within the defined length increment.

4b) Ordination of prey biomass at fish length increments defined in Figure 4a. Data labels are fish length increments. Defined size classes are enclosed.

5a) Cluster analysis



5b) Principal components analysis

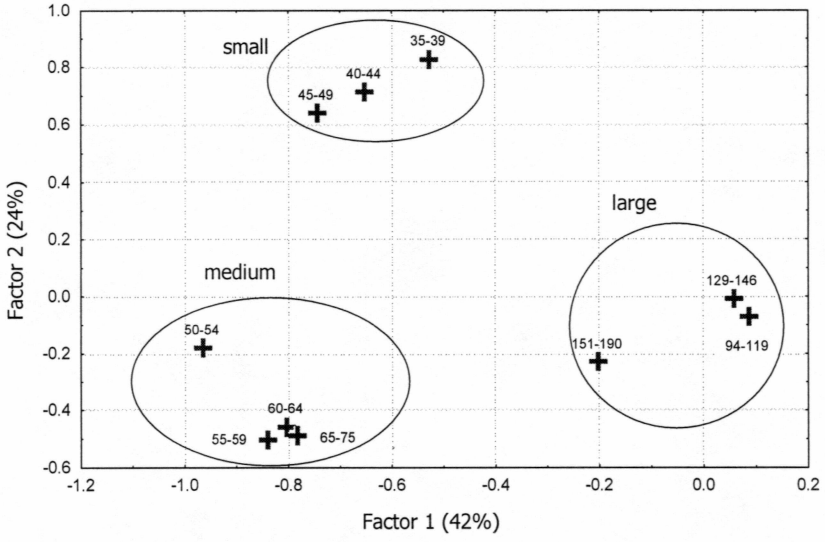
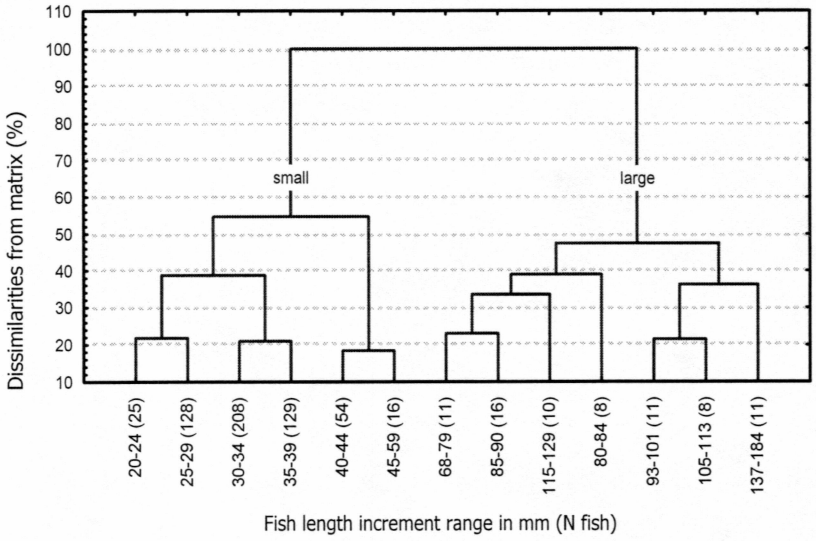


Figure 5. Analysis of Pacific halibut diet by fish length, using a) cluster analysis and b) principal components analysis.

5a) Y-axis distances reflect differences between proportional prey biomass indices at increments of fish total length; data are pooled over all predators within the defined length increment.

5b) Ordination of prey biomass at fish length increments defined in Figure 5a. Data labels are fish length increments. Defined size classes are enclosed.

6a) Cluster analysis



6b) Principal components analysis

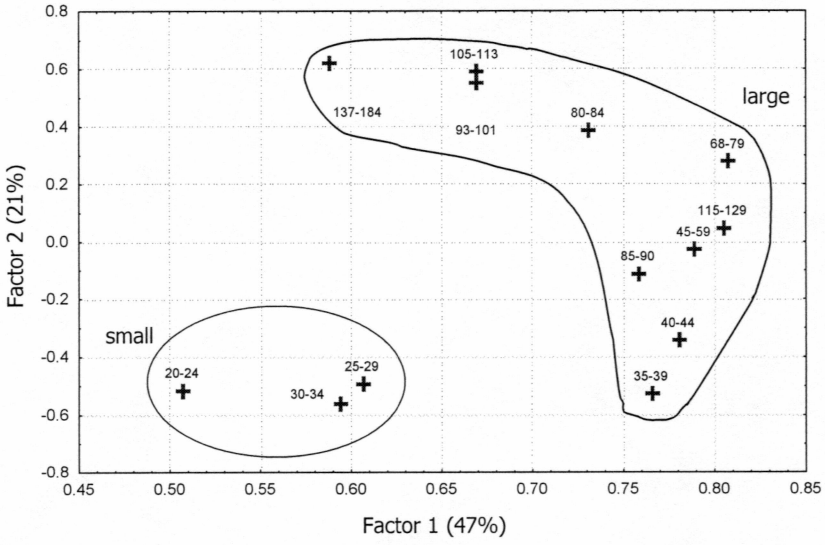
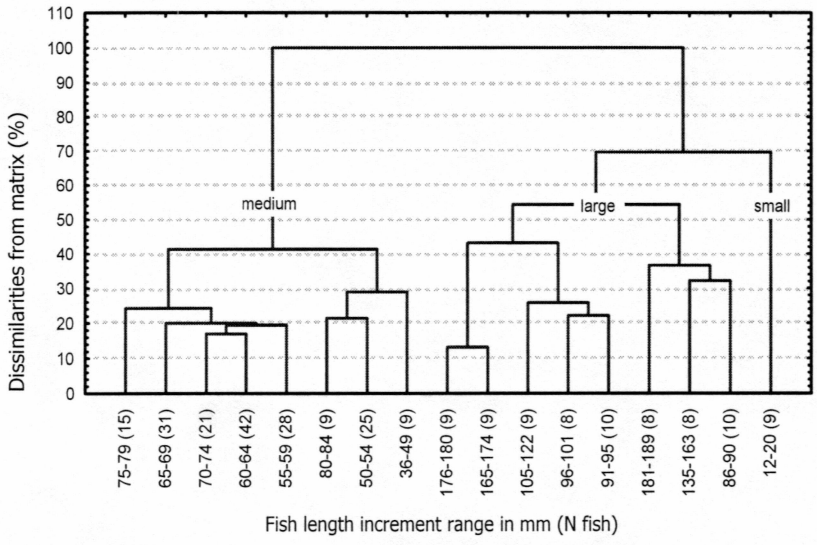


Figure 6. Analysis of rock sole diet by fish length, using a) cluster analysis and b) principal components analysis.

6a) Y-axis distances reflect differences between proportional prey biomass indices at increments of fish total length; data are pooled over all predators within the defined length increment.

6b) Ordination of prey biomass at fish length increments defined in Figure 6a. Data labels are fish length increments. Defined size classes are enclosed.

7a) Cluster analysis



7b) Principal components analysis

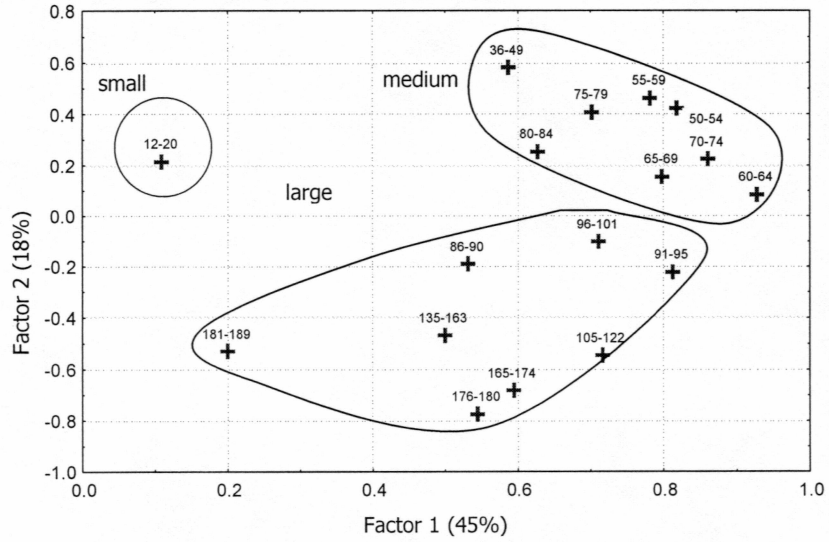


Figure 7. Analysis of yellowfin sole diet by fish length, using a) cluster analysis and b) principal components analysis.

7a) Y-axis distances reflect differences between proportional prey biomass indices at increments of fish total length; data are pooled over all predators within the defined length increment.

7b) Ordination of prey biomass at fish length increments defined in Figure 7a. Data labels are fish length increments. Defined size classes are enclosed.

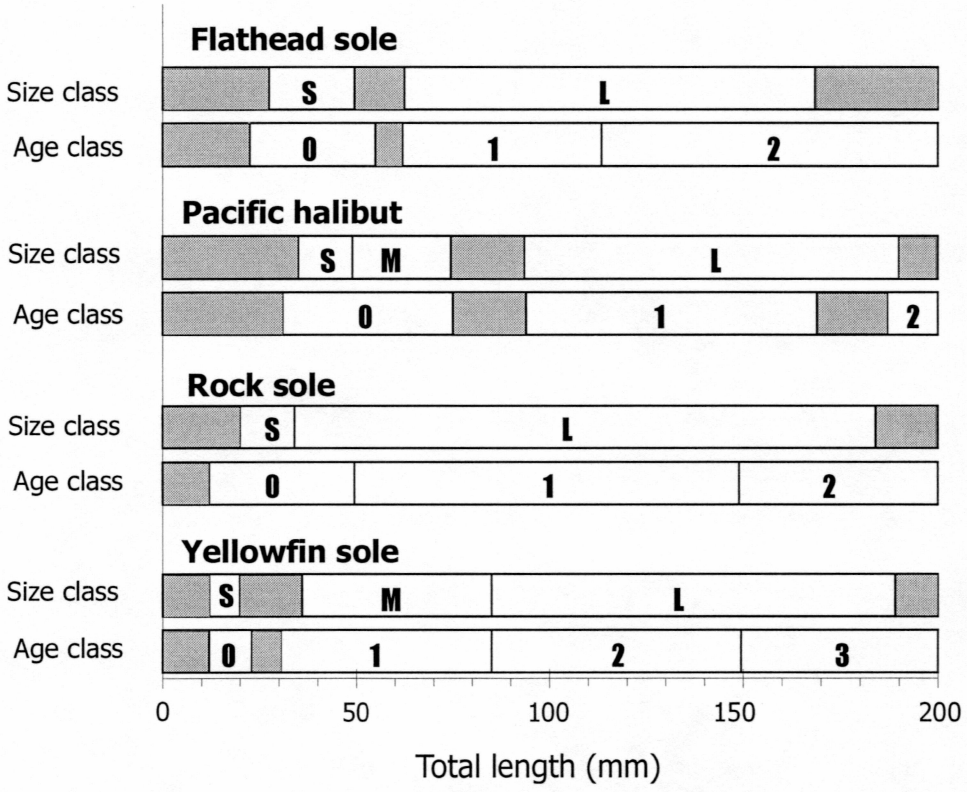


Figure 8. Contrast of fish total length among size classes defined based on diet (this study) and length-at-age (Norcross *et al.*, 1993, 1995). Fishes were collected 11-25 August 1991. Length-at-age data were primarily derived from length frequency analysis. Small, medium and large size classes are abbreviated as S, M, and L, and ages are indicated by the numbers 0, 1, 2, and 3. Shaded areas represent no fishes examined.

Table 1. Number of fish within each species which consumed each prey taxon; only fish with stomach contents are included. Rows in bold font summarize data on pooled prey taxa; the numbers in bold font do not equal the sum of the numbers below when a fish ate prey from more than one taxon within the group. Taxa are arranged in decreasing order of resource utilization; order is alphabetical within each pooled prey taxon. Common and scientific nomenclature is after ITIS (2001).

Pooled prey taxa		Flathead sole N=259	Pacific halibut N=195	Rock sole N=635	Yellowfin sole N=260	All fishes N=1,349
Amphipods	**Amphipoda, all taxa**	**136**	**91**	**302**	**171**	**700**
	Gammaridea					
	Ampelisca spp.		4	4		8
	Ampithoe spp.			22		22
	Anisogammarus pugettensis	1	8	8	3	20
	Anisogammarus spp.			1		1
	Atylus collingi		11	4		15
	Corophium spp.		1	2	1	4
	Dulchia falcata				1	1
	Eohaustorius spp.		1	23		24
	Grandifoxus acanthinus		2	4		6
	Guernea sp.				1	1
	Hippomedon spp.		1	3	2	6
	Ischyrocerus sp.				1	1
	Melita dentata		1			1
	Melita spp.			2	1	3
	Monoculodes spp.	93	19	31	57	200
	Orchemene spp.		1	11	1	13
	Photis spp.			5		5
	Pleustes sp.		1			1
	Pontogeneia spp.		3	2		5
	Pontoporeia femorata			2	3	5
	Protomedeia spp.	2	12	44	44	102
	Unid. Argissidae			1		1
	Unid. Gammaridae *	22	36	7	36	101
	Unid. Gammaridea *	28	16	25	76	145
	Unid. Oedicerotidae	3		1	1	5
	Unid. Pleustidae		2	1	2	5
	Unid. Stenoithoidae				1	1
	Unid. Caprellidea	1	1	3	12	17
Copepods	**Copepoda, all taxa**	**28**	**10**	**346**	**108**	**492**
	Calanoida					
	Acartia spp.			1	5	6
	Calanus spp.			2		2
	Centropages abdominalis		1	14	47	62
	Pseudocalanus spp.	1		8	2	11
	Unid. Aetideidae	3			1	4
	Unid. Calanoida	3		7	4	14
	Unid. Harpacticoida	25	10	344	102	481
	Unid. Cyclopoida			2		2
Cumaceans	**Cumacea, all taxa**	**33**	**75**	**201**	**72**	**381**
	Cumella spp.				2	2
	Cumella vulgaris	2	1		2	5
	Lamprops quadriplicata	19	23	52	46	140
	Lamprops sarsi		1			1
	Lamprops spp.			19		19
	Leucon spp.				3	3
	Unid. Cumacea *	11	1	14	26	52
	Unid. Diastylidae	2	48	41	2	93
Opossum shrimps (Mysids)	**Unid. Mysidae ***	**92**	**77**	**146**	**10**	**325**
Ostracods	**Unid. Ostracoda**	**3**	**1**	**98**	**54**	**156**

Table 1. Continued.

Pooled prey taxa		Flathead sole N=259	Pacific halibut N=195	Rock sole N=635	Yellowfin sole N=260	All fishes N=1,349
Shrimp	**Caridea, all taxa**	**75**	**44**	**12**	**10**	**141**
	Unid. Crangonidae *	35	28	5	10	78
	Crangon alaskensis		1			1
	Unid. Hippolytidae *	39	13	6		58
	Unid. Pandalidae *	8	7	1		16
Crabs	**Anomura & Brachyura, all taxa**	**6**	**31**	**27**	**13**	**77**
	Cancer magister		1			1
	Hyas lyratus		1			1
	Oregonia bifurca		1	3	1	5
	Unid. Brachyura		3	4	1	8
	Unid. Brachyura (zoeae)		1	8	1	10
	Unid. Paguroidea *	6	2	13	9	30
	Unid. Pinnotheridae				1	1
Isopods	**Isopoda, all taxa**	**10**	**1**	**10**	**12**	**33**
	Gnorimosphaeroma oregonense		1			1
	Unid. Flabellifera	9		3	7	19
	Unid. Isopoda	1		7	5	13
Krill	**Euphausiacea, all taxa**	**2**	**2**	**11**	**2**	**17**
	Thysanoessa raschii	1		5	2	8
	Unid. Euphausiacea *	1	2	6		9
Crustacea (Other)	**Crustacea, all other taxa**	**29**	**29**	**32**	**16**	**106**
	Barnacle (Cirripedia, fragment)			2	3	5
	Barnacle (Cirripedia cyprid)			1		1
	Barnacle (Cirripedia nauplius)			1		1
	Unid. Chironomidae				1	1
	Unid. Cladocera		1		2	3
	Unid. Crustacea (fragment)	7	21	22	8	58
	Unid. Malacostraca	22	7	5	2	36
	Unid. Tanaidacea			1		1
Polychaetes	**Polychaeta, all taxa**	**21**	**12**	**212**	**119**	**364**
	Eteone sp.			1		1
	Lumbrineris spp.	1	2	11	19	33
	Nephtys sp.			1		1
	Pectinaria spp.			1	5	6
	Trochochaeta sp.	1				1
	Unid. Ampharetidae			2		2
	Unid. Goniadidae			5	3	8
	Unid. Opheliidae			33	44	77
	Unid. Phyllodocidae			1		1
	Unid. Polychaeta*	17	8	131	85	241
	Unid. polychaete A**	1		34	12	47
	Unid. Polynoidae		1	14	6	21
	Unid. Spionidae		1			1
	Unid. Terebellidae	1		16	9	26
Mollusks	**Mollusca, all taxa**	**52**	**3**	**111**	**67**	**233**
	Unid. Nudibranchia			3		3
	Gastropoda					
	Limacina spp.			2		2
	Littorina sp.				1	1
	Retusa spp.			1	1	2
	Rimula sp.			1		1
	Unid. Gastropoda *		2	11	7	20
	Unid. Gastropoda (egg case)				1	1

Table 1. Continued.

Pooled prey taxa		Flathead sole N=259	Pacific halibut N=195	Rock sole N=635	Yellowfin sole N=260	All fishes N=1,349
Mollusks (continued)	Bivalvia					
	Axinopsida spp.			3	3	6
	Clinocardium spp.				2	2
	Lyonsia spp.			1	3	4
	Nucula sp.				1	1
	Scallop (*Clamys* sp.)				1	1
	Unid. Bivalvia *	1		55	36	92
	Unid. Bivalvia (siphon)	51	1	48	19	119
	Unid. Myidae				1	1
	Unid. Nuculanidae			1	11	12
	Unid. Tellinidae			1		1
	Unid. Thyasiridae				1	1
Fishes	**Teleostei, all taxa**	**2**	**12**	**3**	**1**	**18**
	Flatfishes (Unid. Pleuronectidae)		4			4
	Pacific cod (*Gadus macrocephalus*)		1			1
	Rock sole (*Lepidopsetta polyxystra* or *Pleuronectes bilineatus.*)		2	1		3
	Sculpins (Unid. Cottidae)	1	5			6
	Fish eggs (Unid. Teleostei)				1	1
	Unid. Teleostei	1	3	2		6
Anemone	**Anemone**	**0**	**1**	**1**	**0**	**2**
Arrow worms	**Unid. Chaetognatha**	**14**	**0**	**0**	**0**	**14**
Brittlestars	**Unid. Ophiuroidea**	**0**	**0**	**2**	**1**	**3**
Bryozoans	**Unid. Ectoprocta**	**0**	**0**	**1**	**0**	**1**
Forams	**Unid. Foraminifera**	**0**	**0**	**8**	**2**	**10**
Kinorhynchs	**Unid. Kinorhyncha**	**0**	**0**	**1**	**0**	**1**
Oligochaetes	**Unid. Oligochaeta**	**0**	**0**	**0**	**1**	**1**
Other	**Unid. Animal tissue**	**2**	**3**	**1**	**1**	**7**

* Taxa which consisted primarily of fragments and juvenile animals.

** Unid. polychaete A was distinguishable from other polychaetes, but could not be identified to family.

Table 2. Contrast of proportional number of fishes which were empty (index of vacuity) between species size classes by t-test of independent samples. The lower left portion of the table contains t-values and asterisks in the upper right portion report significant differences (* indicates $p \leq 0.05$, ** indicates $p \leq 0.001$, empty box indicates no difference). Outlined boxes emphasize within species comparisons.

		N	Vacuity	Flathead sole		Pacific halibut			Rock sole		Yellowfin sole		
				small	large	small	medium	large	small	large	small	medium	large
Flathead sole	small	226	28			**	**		**	**		*	
	large	123	22	-1.2		*	**		**				
Pacific halibut	small	91	2	-5.3	-4.3							*	*
	medium	80	0	-5.5	-4.7	-1.3						*	*
	large	30	13	-1.7	-1.0	2.5	3.5						
Rock sole	small	364	1	-10.7	-8.5	-0.6	1.1	-4.3		*		**	*
	large	309	11	-5.2	-3.1	2.5	3.1	-0.4	5.3				
Yellowfin sole	small	9	0	-1.1	-0.8	1.5	3.1	-0.2	2.3	0.0			
	medium	223	18	-2.4	-0.8	3.9	4.2	0.7	7.8	2.5	0.6		
	large	87	20	-1.5	-0.4	3.9	4.4	0.8	7.5	2.2	0.6	0.2	

Table 3. Contrast of the stomach fullness between fishes by t-test of independent samples. The lower left portion of the table contains t-values and asterisks in the upper right portion report significant differences (* indicates $p \leq 0.05$, ** indicates $p \leq 0.001$, empty box indicates no difference). Outlined boxes emphasize within species comparisons.

		N	Fullness (%)		Flathead sole		Pacific halibut			Rock sole		Yellowfin sole		
			Mean	StDev	small	large	small	medium	large	small	large	small	medium	large
Flathead sole	small	163	65	25			**	**		**	**	*	**	**
	large	96	65	27	-0.1		**	**		*	*	*	*	**
Pacific halibut	small	89	82	24	-5.2	-4.4				*	*	**	**	**
	medium	80	83	20	-5.5	-4.8	-0.3			*	*	**	**	**
	large	26	75	22	-1.9	-1.7	1.4	1.7				**	**	**
Rock sole	small	359	74	24	-4.1	-3.2	2.7	3.0	0.1			**	**	**
	large	276	75	27	-3.8	-3.0	2.2	2.5	0.0	-0.3		**	**	**
Yellowfin sole	small	9	37	29	3.2	3.0	5.2	6.1	4.0	4.6	4.1			
	medium	180	54	30	3.5	3.0	7.5	7.8	3.3	8.4	7.6	-1.7		*
	large	71	46	25	5.2	4.7	9.2	10.0	5.2	9.0	8.1	-1.0	2.1	

Table 4. Contrasts of diet diversity between fishes by t-test of independent samples. Diet diversity measure is the Shannon-Wiener index (Smith, 1986). The lower left portion of the table contains t-values and asterisks in the upper right portion report significant differences (* indicates $p \leq 0.05$, ** indicates $p \leq 0.001$, empty box indicates no difference). Outlined boxes emphasize within species comparisons.

		N	Dietary diversity		Flathead sole		Pacific halibut			Rock sole		Yellowfin sole		
			Mean	StDev	small	large	small	medium	large	small	large	small	medium	large
Flathead sole	small	163	0.25	0.32		**	*	**	**	**	**		**	**
	large	96	0.56	0.38	-7.0		**	*				*		*
Pacific halibut	small	89	0.34	0.40	-2.0	3.7			**	**	**		**	**
	medium	80	0.44	0.43	-3.8	2.0	-1.5		*		*		*	**
	large	26	0.67	0.43	-5.9	-1.3	-3.5	-2.4				*		
Rock sole	small	359	0.55	0.44	-7.5	0.4	-3.8	-1.8	1.5			*		*
	large	276	0.56	0.47	-7.9	-0.4	-4.2	-2.4	0.9	-1.1		*		*
Yellowfin sole	small	9	0.08	0.23	0.9	3.1	1.4	1.9	3.3	2.6	2.7		*	**
	medium	180	0.59	0.46	-7.7	-0.5	-4.2	-2.4	0.9	-1.1	-0.1	-2.8		*
	large	71	0.70	0.47	-8.8	-2.4	-5.4	-3.8	-0.4	-3.0	-2.1	-3.5	-2.0	

Table 5. Proportional dietary overlap between species size class pairs (after Schoener, 1970). The lower left portion of the table contains percentage of overlap in prey biomass and the upper right portion indicates relative dietary overlap (no shading indicates <20% overlap, light gray indicates 20-50% overlap, and dark gray indicates >50% overlap). Outlined boxes emphasize within species comparisons.

	Size	N fish	Flathead sole		Pacific halibut			Rock sole		Yellowfin sole		
			small	large	small	medium	large	small	large	small	medium	large
Flathead sole	small	163										
	large	96	41									
Pacific halibut	small	89	36	37								
	medium	80	28	66	44							
	large	26	12	28	21	23						
Rock sole	small	359	33	23	31	28	8					
	large	276	40	35	38	39	12	59				
Yellowfin sole	small	9	3	0	2	0	0	19	9			
	medium	180	41	20	30	22	8	40	53	6		
	large	71	26	22	20	16	12	41	48	3	45	

Table 6. Mean ± standard deviation of fish density (number of fish/100 m^2) values at each habitat. The significance columns indicate habitats where density values were significantly different ($p<0.05$); each habitat is represented by a code in this column, e.g., abundance of small flathead sole on shallow gravel (a) is different from deep sand (e) and deep mud (f). Bold font indicates significantly high density of fish.

Habitat code	All habitats			Shallow gravel a		Shallow sand b		Shallow mud c		Deep gravel d		Deep sand e		Deep mud f	
	CPUE	F-value	p-level	CPUE	Sig	CPUE	Sig	CPUE	Sig	CPUE	Sig	CPUE	Sig	CPUE	Sig
Small flathead sole	2.6 ± 4.4	10.5	<0.0001	0.4 ± 1.3	ef	1.3 ± 3.4	ef	1.7 ± 2.7	e	8.5 ± 10.0		**6.7 ± 5.3**	**abc**	**6.7 ± 4.3**	**ab**
Large flathead sole	2.8 ± 4.3	14.0	<0.0001	1.8 ± 3.4	f	0.5 ± 2.0	ef	5.0 ± 5.5		6.0 ± 7.9		**5.4 ± 4.5**	**b**	**7.8 ± 3.5**	**ab**
Small halibut	1.6 ± 3.5	1.5	0.2	1.0 ± 2.7		2.4 ± 3.8		2.1 ± 3.1		0.0		1.8 ± 5.5		0.0	
Medium halibut	1.5 ± 3.2	3.4	<0.01	0.7 ± 2.0		2.8 ± 3.9		1.1 ± 3.2		0.0		0.0		0.0	
Large halibut	0.4 ± 1.5	0.6	0.66921	0.6 ± 2.2		0.6 ± 1.6		0.4 ± 1.1		0.0		0.0		0.0	
Small rock sole	6.1 ± 6.8	6.3	<0.0001	2.6 ± 4.8	b	**9.2 ± 6.9**	**af**	7.4 ± 6.7		0.0		6.2 ± 8.5		1.4 ± 2.7	b
Large rock sole	7.4 ± 7.4	18.7	<0.0001	3.2 ± 4.8	b	**12.4 ± 6.6**	**aef**	**9.9 ± 5.1**	**ef**	0.0		1.9 ± 3.3	bc	0.6 ± 2.5	bc
Small yellowfin sole	0.3 ± 1.3	0.3	0.89071	0.1 ± 0.5		0.5 ± 1.7		0.3 ± 1.0		0.0		0.6 ± 1.8		0.2 ± 0.8	
Medium yellowfin sole	5.5 ± 7.0	14.6	<0.0001	2.9 ± 6.3	c	**7.6 ± 6.5**	**cf**	**16.2 ± 4.1**	**abdef**	0.0	c	0.2 ± 0.6	c	0.0	bc
Large yellowfin sole	2.1 ± 4.3	14.3	<0.0001	2.3 ± 4.5	c	1.2 ± 2.7	c	**11.0 ± 6.2**	**abdef**	0.0	c	0.0	c	0.8 ± 2.4	c
N collection sites	105			21		48		9		3		9		15	

Table 7. Results of one-way ANOVA tests contrasting diets of a single species size class among habitats (F-values). Vacuity tests include all fish and habitats examined. Proportional fullness and diet diversity tests include only the habitats where ≥6 fish contained prey; see Table 6 for habitat codes. Asterisks indicate significant differences among habitats (* p≤0.05, ** p≤0.001).

Species	Size class	Vacuity	Habitats ≥6 fish had fed	Proportional fullness	Diet diversity
Flathead sole	small	1.37	bcdef	0.71	2.40 *
	large	3.61 *	bdef	3.52 *	2.86 *
Pacific halibut	small	0.57	abe	6.62 **	7.78 **
	medium	Not applicable	ab	0.37	1.77
	large	0.92	ab	6.05 *	6.42 *
Rock sole	small	0.49	abcef	3.42 *	2.93 *
	large	0.79	abce	6.25 **	1.27
Yellowfin sole	medium	2.41	abc	3.16 *	1.99
	large	2.06	abc	3.35 *	2.03

Table 8. Prey taxon frequency of occurrence at depth–sediment habitats. Symbols indicate prey taxa consumed by ≥25% of fish within at least one species size class (x), and those consumed by <25%, but at least N=2, fish of a single species size class (–). Blank cells indicate habitats where the prey taxon was eaten by 0–1 fish of any species size class.

	Shallow			Deep		
	gravel	sand	mud	gravel	sand	mud
Amphipods	x	x	x	x	x	x
Copepods	x	x	x	–	x	x
Cumaceans	x	x	x		x	–
Opossum shrimps	x	x	–	x	x	x
Ostracods	x	x	x		x	
Shrimp	x	x		x	x	x
Crabs	x	x	–	–	x	
Isopods		–	–		–	–
Krill		–				–
Polychaetes	x	x	x	–	x	–
Mollusks	x	–	x	x	–	x
Fishes	x	–				

Table 9. Prey taxon frequency of occurrence within each species size class. Symbols indicate prey taxa consumed by ≥25% of fish in at least one depth–sediment habitat (x), and those consumed by <25%, but at least N=2, fish (–). Blank cells indicate where the prey taxon was eaten by 0–1 fish at any habitat.

	Flathead sole		Pacific halibut			Rock sole		Yellowfin sole	
	small	large	small	medium	large	small	large	medium	large
Amphipods	x	x	x	x	x	x	x	x	x
Copepods	x		–			x	x	x	x
Cumaceans	x	x	x	x		x	x	x	x
Opossum shrimps	x	x	x	x		x	x	–	
Ostracods						x	–	x	x
Shrimp	x	x	–	x	x	–	–	–	–
Crabs		–	–	x	x	–	x	–	
Isopods	–						–	–	
Krill							–	–	
Polychaetes	–	–	x	–	–	x	x	x	x
Mollusks	x	x				x	x	–	x
Fishes					x				

Table 10. Differences in presence of prey taxa among the fishes at one habitat (Friedman ANOVA). Species size classes are limited to those where N>_6 fish at the habitat. No significant differences in prey composition were found.

Habitat	Species size classes tested	df	χ^2	p
Shallow gravel	small, medium, and large Pacific halibut small and large rock sole medium and large yellowfin sole	6	6.1	0.4
Shallow sand	small and large flathead sole small, medium, and large Pacific halibut small and large rock sole medium and large yellowfin sole	8	11.6	0.1
Shallow mud	small and large rock sole medium and large yellowfin sole	3	5.3	0.2
Deep gravel	small and large flathead sole	1	0.1	0.7
Deep sand	small and large flathead sole small Pacific halibut small and large rock sole	4	4.8	0.3
Deep mud	small and large flathead sole small rock sole	2	4.1	0.1

Table 11. Differences in presence of prey taxa eaten by one species size class over different habitats (Friedman ANOVA). Habitats were limited to those where N>_6 fish contained prey. An asterisk indicates significant difference in diet among habitats ($p<0.05$).

Species size class	Habitats tested	df	χ^2	p
Small flathead sole	shallow sand deep gravel, deep sand, deep mud	3	5.4	0.1
Large flathead sole	shallow sand deep gravel, deep sand, deep mud	3	2.2	0.5
Small Pacific halibut	shallow gravel, shallow sand deep sand	2	8.2	0.02 *
Medium Pacific halibut	shallow gravel, shallow sand	1	0.1	0.8
Large Pacific halibut	shallow gravel, shallow sand	1	2.0	0.2
Small rock sole	shallow gravel, shallow sand, shallow mud deep sand, deep mud	4	14.1	0.01 *
Large rock sole	shallow gravel, shallow sand, shallow mud deep sand	3	5.7	0.1
Medium yellowfin sole	shallow gravel, shallow sand, shallow mud	2	1.2	0.5
Large yellowfin sole	shallow gravel, shallow mud	1	0.1	0.8

Table 12. Frequency of occurrence (FO) of prey taxa in the stomachs of small rock sole (sRS) and small Pacific halibut (sPH) is indicated at different habitats. Prey taxa are indicated (x) where two criteria are met: a relatively low number of fish within the species size class ($\leq$25%) ate the prey relative to the proportion of other fishes which ate the prey at that habitat, and the species size class under consideration had $\geq$25% FO of that prey taxon at a different habitat. Data are limited to the habitats where N$\geq$6 fish contained prey. Total length (mean $\pm$ standard deviation) of fishes analyzed for diet is reported.

Prey	Shallow gravel		Shallow sand		Shallow mud	Deep sand		Deep mud
taxon	sPH	sRS	sPH	sRS	sRS	sPH	sRS	sRS
Amphipods	58	33	60	44	22 x	4 x	38	33
Copepods	0	90	20	79	67	0	36	56
Cumaceans	79	24 x	30	25	0 x	100	51	22
Opossum shrimps	5 x	52	30	24 x	22	4 x	3 x	11 x
Ostracods	0	14 x	3	27	11 x	0	25	0
Shrimp	0	0	20	2	0	12	0	0
Crabs	0	0	10	2	0	0	0	0
Isopods	0	0	0	0	0	0	6	0
Krill	0	0	3	1	0	0	0	0
Polychaetes	26	14 x	3 x	38	67	0 x	15 x	0 x
Mollusks	0	31	0	18	0 x	0	17	56
Fishes	0	0	0	0	0	0	0	0
N fish	19	41	40	199	12	25	101	6
Total length (mm)	46 $\pm$ 4	33 $\pm$ 2	43 $\pm$ 4	30 $\pm$ 3	29 $\pm$ 3	41 $\pm$ 4	28 $\pm$ 3	26 $\pm$ 2

Table 13. One-way ANOVA comparing proportional fullness among species size classes and habitats, and two-way ANOVA interaction of these two factors (F values). The interaction term is limited to habitats where ≥6 fish of each size class contained prey, and consequently no small yellowfin sole are included. Signicance is noted (* $p \leq 0.05$, ** $p \leq 0.001$).

Species	Size class	Habitat	Size class x Habitat
Flathead sole	<0.0	1.0	2.5
Pacific halibut	1.4	4.5 *	2.6
Rock sole	0.1	3.2 *	5.6 **
Yellowfin sole	3.3 *	2.3	5.7 *

Table 14. One-way ANOVA comparing diet diversity among species size classes and habitats, and two-way ANOVA interaction of these two factors (F values). The interaction term is limited to habitats where ≥6 fish of each size class contained prey, and consequently no small yellowfin sole are included. Signicance is noted (* $p \leq 0.05$, ** $p \leq 0.001$).

Fish	Size class	Habitat	Size class x Habitat
Flathead sole	48.3 **	2.8 *	3.0 *
Pacific halibut	6.1 *	5.5 **	5.2 *
Rock sole	<0.0	4.0 *	0.3
Yellowfin sole	7.5 **	3.9 *	0.3